Biased estimates of fitness consequences of brood size manipulation through correlated effects on natal dispersal

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Summary

1. Dispersal of parents and offspring in relation to manipulated brood size were analysed in the great tit Parus major (L.) to study the potential confusion between dispersal and survival. The study area consisted of eight woodlots interspersed with nonbreeding habitat. The maximum distance between nestboxes was 10 km.
2. The brood size of pairs with similar clutch size and laying date was manipulated in 3 years when chicks were 2 days old (1995, 1997 and 1998). Three nestlings were removed from one and added to another brood while a third was kept as a control. Offspring were measured, weighed and marked and breeding birds were captured and marked to allow dispersal estimates.
3. For the offspring, dispersal was estimated as the distance between the natal nestbox and the nestbox of first breeding (natal dispersal distance) and, for the parents, as the distance between breeding boxes in two subsequent seasons (breeding dispersal distance).
4. Natal dispersal distance was positively affected by brood size manipulation. This effect was more pronounced in males than in females. Breeding dispersal distance was not affected by manipulation.
5. The practical consequence of this finding is that fitness estimates used to measure selection on brood size did depend on the spatial scale of the study area. For the Lauwersmeer population measured selection pressure changed from positive to stabilizing when I restricted the spatial scale of recovery. Other brood size manipulation experiments may suffer from similar biases in their fitness estimates.
6. The biological consequence of this finding is that, if clutch size has a heritable component, local adaptation of clutch size will depend on the spatial heterogeneity of the habitat.

Key-words: brood size manipulation, dispersal, fitness, Parus major, selection.


Introduction

Dispersal is the movement of individuals that cause a redistribution of organisms over the habitat. It often takes place between birth and first reproduction. Both the cost and the benefits of dispersal such as inbreeding avoidance, avoidance of intra-specific and kin competition and redistribution over resources are important selection pressures shaping natal dispersal behaviour (Hamilton & May 1977; Greenwood & Harvey 1982; Hanski 1998; Gandon & Michalakis 2001; Perrin & Goudet 2001). Evolutionary processes such as local adaptation and specialization will be affected by dispersal (Clobert et al. 2001; Lenormand 2002) and this makes the understanding of the ecological and evolutionary background of dispersal an important task in evolutionary ecology.

In birds dispersal on the individual level has been studied in relation to variation in traits such as fledgling mass (Greenwood, Harvey & Perrins 1979; Drent 1984; Nilsson 1989; Verhulst, Perrins & Riddington 1997; Alteweg, Ringsby & Saether 2000; van der Jeugd
The studies mentioned above except the European kestrel study (Daan et al. 1990) implicitly assume that fitness estimates of the alternative behavioural options are not differentially affected by dispersal (Perrins 1965; Nur 1984a). When natal dispersal distance (the distance between the place of birth and the place of first breeding) is the outcome of lost competition over some distance between the place of birth and the place of first settlement and residency (Stamps 2001; Doligez, Danchin & Clobert 2002a).

Given that birds easily move between the study plot and the surroundings unbiased estimates of dispersal are difficult to get (Koenig et al. 1992; Lambrechts et al. 1999; Doligez et al. 2002b). Studies tend to be undertaken in plots that consist of a part of a larger system and thus cannot adequately assess the effects of dispersal on fitness (Kenward, Marcstrom & Karlbom 1993). In evolutionary studies that quantify fitness consequences of behavioural alternatives, differential dispersal may bias the measures of fitness. One example is the rigid experimental approach that has been taken to study the effects of experimental changes of brood size. It is an excellent model to study fitness consequences of variation in reproductive strategies. The reproductive strategy is represented by the brood size, and the fitness consequences of alternative options can be estimated through manipulation of the brood size. Results indicate that in some populations adaptation of clutch size exists, as in the collared flycatcher Ficedula albicollis (L.) (Gustafsson & Sutherland 1988) and in the great tit (Lindén 1990; Tinbergen & Daan 1990; Both, Tinbergen & Visser 2000). Others claim that birds are even able to produce a brood size that maximizes their individual fitness (individual optimization of brood size). This is the case in the great tit (Perrins & Moss 1975; Pettifor, Perrins & McCleery 1988, 2001), in the European kestrel Falco tinnunculus (L.) (Daan, Dijkstra & Tinbergen 1990) and in the blue tit Parus caeruleus (L.) (Pettifor 1993a,b). In one study on great tits individual optimization could not be shown to exist (Tinbergen & Both 1999) and other studies even conclude that clutch size was not locally adapted as in the blue tit (Nur 1986) and in the great tit (Verhulst 1995; Tinbergen & Sanz 2004). Gene flow and habitat heterogeneity have been proposed to explain why birds sometimes fail to produce locally adapted clutch sizes because clutch size could be more adapted to the ecological situation in the source than in the sink population (Dias & Blondel 1996; Lenormand 2002).

The studies mentioned above except the European kestrel study (Daan et al. 1990) implicitly assume that fitness estimates of the alternative behavioural options are not differentially affected by dispersal (Perrins 1965; Nur 1984a). When natal dispersal distance (the distance between the place of birth and the place of first breeding) is the outcome of lost competition over some local resource, brood size enlargement may have a positive effect on natal dispersal through a negative effect on body condition. A different scenario such as enhanced kin competition independently of nestling mass could generate a similar pattern with brood manipulation. However, the actual pattern should also depend on local habitat quality as compared with the habitat quality of the alternatives. Adult dispersal between breeding seasons could be affected by brood size manipulation because parents may react to a lowered breeding success by dispersing to a different breeding site.

The aim of this paper is to detect whether dispersal of both parents and offspring was causally related to brood size, and, if so, how dispersal biases brood size related fitness estimates. The biological relevance of the patterns found will be discussed.

**Methods**

**STUDY AREA AND STUDY SPECIES**

The study was carried out on great tits in woodlots of young, mixed deciduous forest in the Lauwersmeer, the Netherlands (53°20′N, 06°12′E. Fig. 1), reclaimed from the Wadden Sea in 1968. Due to a rapid succession the area changed from bare sand to a rich habitat for waterfowl and songbirds (Altenburg et al. 1985). Woodlots were planted in the higher areas starting in 1973, and from 1993 onwards about 200 nestboxes were available in eight plots of different size (6–106 ha) interspersed with nonbreeding habitat consisting of grazed areas, reed beds and water (Fig. 1). Few natural holes were available so that the majority of breeding attempts in our plots was in the nestboxes. Five plots in the north were isolated by distance from three plots in the south by about 3–5 km. For further details see Sanz & Tinbergen (1999) and Tinbergen & Sanz (2004).

The occupation of nest boxes by great and blue tits in the Lauwersmeer was relatively high (70–90%). Great tits laid about 10 eggs (average 1993–98: 9.73, SD = 1.22, n = 565) and first broods were followed in 11–51% of the cases by second broods (average 1993–98: 37%). No beech crop Fagus silvatica (L.) was available as winter food and it was observed that wintering birds ate sand-dorn berries Hippophae rhamnoides (L.).

**CAPTURE–RECAPTURE**

From the beginning of April we did weekly nest checks. Daily nest visits around the expected day of hatching allowed estimates of the hatching date. When the young were 7–10 days old (day of hatching = 0) both parents were captured with spring traps and ringed (if unringed), and measured for body mass (to the nearest 0.1 g) and tarsus (for the nearest 0.1 mm) and their young ringed. When the young were 14 days old they were weighed and their tarsus and wing length measured.

**BROOD SIZE MANIPULATION**

Manipulation of brood size was carried out 2 days after the nestlings hatched as described before (Sanz & Tinbergen 1999; Tinbergen & Sanz 2004). Three...
nestlings were transferred between nests to create reduced and enlarged broods. For each experimental pair of nests there was a control brood where brood size was not altered (number of broods 1995, 51; 1997, 66; and 1998, 51).

ESTIMATES OF DISPERAL DISTANCE
Nestbox positions were recorded with the use of detailed maps from the woodlots. The distance between the natal box and the box of first breeding was named natal dispersal distance. The distance between the boxes occupied in two consecutive breeding seasons was named breeding dispersal distance and measured in metres.

SPATIAL SCALE AND FITNESS ESTIMATES
The fragmented structure of the Lauwersmeer population (Fig. 1) is especially suitable to analyse how recapture distance may affect fitness estimates. I analysed whether an artificial reduction of the distance of recapture affected our estimates of the direction of selection on brood size. For different maximal recapture distances between the natal nestbox and the nestbox of first breeding (< 10 km, < 750 m, < 250 m) the number of recruits per nest for each of the manipulation categories was recalculated (reduced, control and enlarged). In this way I mimicked how a reduction in area of search would affect recapture rates.

Similar calculations were done for the brood size manipulations in the Hoge Veluwe population of great tits, which have been reported earlier (Tinbergen & Daan 1990; Tinbergen & Sanz 2004). This study area differed in structure from the Lauwersmeer in that it consisted of one plot with nestboxes situated within a larger area of similar habitat. The study area itself was presumably more suitable for breeding because ample nestboxes were available, in contrast to the direct surroundings. The natal dispersal for this data set (n = 348 broods) was analysed to get an indication whether effects of brood size manipulation on natal dispersal would show up in this data set.

DATA ANALYSIS
Dispersal distances (in metres) were transformed to normalize variance. For natal dispersal, $10\log(10\log(10\log(distance(m) + 100)))$ was used to normalize the frequency distribution of natal dispersal (Kolmogorov–Smirnov: females $Z = 0.092$, $P > 0.2$; males $Z = 0.093$, $P > 0.2$). For the Hoge Veluwe a $10\log(distance +100)$ transformation was sufficient to normalize data (Kolmogorov–Smirnov $Z = 0.078$, $P > 0.2$).

Dispersal patterns may be the consequence of the spatial arrangement of the nestboxes relative to the positions of the manipulated boxes. This effect was controlled for statistically by including birth plot as a random factor in the analysis. By doing so the effect of manipulations on natal dispersal were compared within plots.

Parents bred in the same box often and in this case dispersal was analysed in two ways. First, the probability to breed in the same box was analysed using logistic

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Fig. 1. Map of the reclaimed area of the Lauwersmeer with the eight nestbox plots. Middle grey areas are wooded areas without nestboxes. The remaining land is unsuitable for great tit breeding.
regression. Because I could not normalize the distribution of breeding dispersal distances of the birds that did not breed twice in the same box by transformation, a nonparametric test was used for all parents to test whether breeding dispersal distances were affected by brood size manipulation. Manipulated nests that were deserted before capture of the parents (n = 6 over 3 years) were not included in the analysis because parents were unknown.

Nestling mass decreased with increasing brood size through manipulation (Sanz & Tinbergen 1999; Tinbergen & Sanz 2004). To test the plausibility of a role of nestling mass as a causal factor it was included in a regression analysis to explain dispersal distance.

In cases where the error structure was binomial and the deviance of the full model was larger than the degrees of freedom, an F-test was used instead of a χ²-test to correct for overdispersion. Means are given ± SD.

**Results**

**PARENTS DISPERSAL DISTANCE**

The probability that parents remained in the same nestbox was 0·30 and independent of manipulation category (logistic regression: effect of sex and manipulation category, respectively, F_{1,102} = 0·188 and F_{1,102} = 0·947, both P > 0·3, controlled for year F_{1,102} = 0·422, P > 0·6, n = 108, deviance null model 131·1). Overall, there was no relation between breeding dispersal distance and manipulation (Kruskall–Wallis, χ² = 3·457, d.f. = 2, P > 0·15, n = 108); the sexes did not differ statistically in their breeding dispersal (Kolmogorov–Smirnov, Z = 1·042, P > 0·2, n = 108). Thus, there was no indication that breeding dispersal was dependent on manipulation (Fig. 2a). Mean breeding dispersal distance was 123 m (± 223, n = 108), which is in the order of magnitude of the distance between two adjacent nestboxes. Breeding birds thus tend to remain in the same area.

**OFFSPRING DISPERSAL DISTANCE**

Mean natal dispersal distance was for males 691 m (± 702 m, n = 66) and for females 1183 m (± 1557 m, n = 62). Natal dispersal was higher than breeding dispersal (Two sample Kolmogorov–Smirnov test, Z = 6·06, P < 0·001).

Brood size manipulation and sex affected natal dispersal distance. Females dispersed further than males. Plot, year or birth date did not significantly reduce the deviance of this model (Table 1, Fig. 2b). An ANOVA on residual dispersal distance after controlling for sex showed that the offspring of reduced broods dispersed significantly less far than the offspring from enlarged broods (Tukey P < 0·05). To control for spatial heterogeneity the (nonsignificant) effect of natal plot in the analysis was included. The results hardly differed when not controlling for plot indicating that the spatial heterogeneity did not affect the outcome of the analysis.

Male offspring from the enlarged broods bred more than twice the distance from their natal box than males from the reduced broods (Fig. 2b). In females natal dispersal distance was less affected by the brood size manipulation than in males (Fig. 2b). This difference between the sexes was not statistically significant (interaction manipulation*sex, F_{2,116} = 2·234, P > 0·1, Table 1). However, when manipulation was used as an ordered variable the interaction was significant (F_{1,115} = 4·592, P < 0·05). Males may have responded more strongly to manipulation. When manipulation was deleted from this model while including nestling mass as an explanatory variable, nestling mass did explain variance in dispersal distance (P < 0·02). This model (with nestling mass and sex) explained slightly less variation than the previous model with manipulation and sex (R² = 0·105 vs. R² = 0·122). Nestling mass may therefore be causally involved in the explanation of the manipulation effect on natal dispersal distance.

**SPATIAL SCALE AND FITNESS ESTIMATES**

Because manipulation affected natal dispersal distance it was expected that the estimate of the fitness consequences of brood size manipulation would depend on the spatial scale of recoveries used. Therefore, the maximum recapture distance for our recruits was reduced artificially in steps (see Methods). With decreasing spatial scale of recovery the recapture probability lowered, as expected, but this reduction was more pronounced for the enlarged category (Fig. 3a). The
fraction of birds caught further than 500 m was significantly related to manipulation when controlled for sex (logistic regression, sex: $F_{1,125} = 8.77$, $P < 0.005$, manipulation as a continuous ordered variable: $F_{1,125} = 4.470$, $P < 0.05$, residual deviance 156.3, d.f. = 125).

I calculated the selection gradient as the number of recruits recovered per nest as a function of manipulation to see whether a reduction of the maximum recapture distance would indeed change our interpretation of the selection pressure on brood size. I tested for nonlinearity by including or excluding manipulation squared in a Poisson regression explaining the number of recruits from manipulation and birth date. In the Lauwersmeer population reduction of the maximal recovery distance from 10 000 m to 750 changed the selection pressure from positive to stabilizing (Table 2).

Similar calculations for the Hoge Veluwe population (Tinbergen & Daan 1990) revealed that natal dispersal within study plot turned out not to depend on brood size manipulation ($F_{2,143} = 1.98$, $P > 0.15$) and that the relation between recruits per nest and brood size manipulation was independent of the distance of recovery used (Fig. 3b, analysis is not shown).

**Discussion**

In this study it was found that the breeding dispersal distance of the parents was not affected by manipulating brood size, but offspring natal dispersal distance was. Offspring of larger broods did disperse further before starting to breed. This increase of natal dispersal distance with brood size can bias the estimate of the brood size that maximizes recruitment.

**Dispersal and Fitness Effects**

Many brood size manipulation studies did use local recovery as component in their fitness estimates. They implicitly assumed that natal dispersal distance was not related to brood size (Nur 1984b; Gustafsson & Sutherland 1988; Smith, Källander & Nilsson 1989; Tinbergen & Daan 1990; Pettifor 1993a; Verhulst 1995; Both et al. 2000; Pettifor et al. 2001), but see Daan et al. (1990) and Doligez et al. (2002b).

The optimal brood size balances the parental fitness costs and benefits associated with brood size to maximize fitness (Charnov & Krebs 1974; Daan & Tinbergen 1997; Tinbergen & Sanz 2004). Dispersal affects the estimate of the optimal brood size in two ways. First, if offspring...
dispersal
Brood size and dispersal

Table 2. Poisson regressions of the number of recruits recovered per brood as a function of brood size manipulation (continuous variable: 1, 2 or 3, respectively, reduced control and enlarged) and its square, controlled for birth date (mean birth date 47). (A) All recovered recruits up to 10 000 m from the natal box and (B) only the recruits recovered within 750 m of the natal nestbox. By reducing the distance of recovery apparent selection changed from directional (A: positive significant Manipulation term and NS Manipulation squared term) to stabilizing (B: positive significant Manipulation term and negative significant Manipulation squared term). Estimated peak recruits per brood at 2.4 manipulation units for B

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When we correct for a brood size independent fraction of dispersal, the fitness of the offspring increases more than the fitness of the parents. This causes the slope of the offspring fitness brood size curve to change more than the slope of the parental fitness brood size curve. This effect shifts the optimal brood size towards larger broods. Studies that find effects of brood size manipulation on local survival of both parents and offspring should therefore correct their fitness estimates for the level of dispersal (like the attempt in Tinbergen & Daan 1990). A second way that dispersal may affect fitness estimates, as shown in this study, is when dispersal distance is affected by brood size. It needs no further arguing that this can seriously affect the conclusions of brood size manipulation studies.

SPATIAL SCALE AND FITNESS ESTIMATES

In earlier work our group showed that the effect of brood size manipulations in great tits varied between studies from support for optimization of clutch size (Tinbergen & Daan 1990) to support for directional selection for either small (Verhulst 1995) or large clutches (Tinbergen & Sanz 2004). These differences in results may be caused by differences in spatial scale of the study areas. Therefore, the fitness consequences of brood size manipulations were reanalysed for both the Lauwersmeer (Tinbergen & Sanz 2004) and the Hoge Veluwe (Tinbergen & Daan 1990) study. Indeed the interpretation that selection pressure on brood size was positive in the Lauwersmeer population, would change to the interpretation that selection pressure was stabilizing if I only used data for recapture distances below 750 m (Fig. 3a). However, for the Hoge Veluwe the estimated selection pressure was independent of the distance of recovery used in the analysis (Fig. 3b). This outcome for the Hoge Veluwe is at first sight reassuring for the earlier mentioned interpretation of the Hoge Veluwe data, namely that selection on clutch size is stabilizing there. Within the study plot no effect of the distance of recovery on selection pressure could be detected; dispersal did not affect the outcome of the brood size manipulation experiments. Still I am not certain because I know that for a stable population in the Hoge Veluwe roughly one of three offspring is expected to breed outside the study area, hence there is still scope for differential dispersal with brood size manipulation on a larger spatial scale. Actual measurements of dispersal distance over a larger area are needed to verify the interpretation of the fitness effects of brood size experiments.

POSSIBLE MECHANISMS OF DISPERAL

In adult blue tits breeding dispersal distance was not affected by brood size manipulation except for females that reared extremely small experimental broods (three young). They moved significantly further than the females from the other experimental categories (Nur 1988). In the pied flycatcher Ficedula hypoleuca (L.) male breeding dispersal distance was not affected by manipulation (Siikamaki, Hovi & Ratti 1997) and that is what was found for the great tit in this study for both males and females. Lindén (1991) found an experimental effect of brood size manipulation on divorce rate in the great tit, which may be interpreted as a reaction to reduced reproductive success or lower territory quality. However, there is a clear case where brood manipulation did affect breeding dispersal distance. On the basis of experimental nestling failure Haas (1998) concluded that American robins Turdus migratorius (L.) had low return rates resulting from breeding dispersal in response to nestling failure.

The variation in natal dispersal distance as a consequence of manipulation could, in the current study, statistically also be explained by variation in nestling mass at the age of 14 days. This signals a potential route for the causal relationship underlying the manipulation...
effect on natal dispersal distance. If competitive ability is negatively affected by the manipulation, the difference between the sexes in the effect of manipulation on natal dispersal distance is interesting (assuming it is not an artefact of the scale of the study). Male great tits compete for territories already from September onwards and for them the manipulation may directly affect their chances. Females are less competitive in this respect and therefore the effect of manipulation may be less pronounced (Drent 1984; Tinbergen et al. 1987). An alternative yet related causal route might operate through the occurrence of coping styles. In the great tit heritable variation in coping styles or personalities occur (Drent, Van Oers & van Noordwijk 2003) and coavity with natal dispersal distance (Dingemanse et al. 2003). Faster personalities coavity with more dispersal. Rearing conditions also modulate great tit personality (Carere 2003). Food restriction in the nest caused faster personalities. Thus competition in the nest through brood size manipulation may lead to lower body mass and subsequently to a faster personality and further dispersal. In a competitive situation dispersal may be the better option for a bird with lower body mass and this adaptive response may be mediated by a shift in personality. It is likely that such effects are related to the body mass relative to the competitors, as has been found for local survival in great tits (Both, Visser & Verboven 1999).

Brood size effects or offspring mass effects on natal dispersal distance are not always found. In the tree swallow Tachycineta bicola (Vieillot) natal dispersal distance was not affected by clutch size manipulation (Shutter & Clark 2003). Also natal dispersal distance did not coavity with nestling body mass (and size) in the collared flycatcher (Pärt 1990), in the marsh tit Parus palustris (L.) (Nilsson 1989) and in the house sparrow Passer domesticus (L.) (Altwegg et al. 2000). Other factors than body mass that were affected by the brood size experiment could be important in the causation of effects on natal dispersal distance such as the intensity of post-fledgling care and within brood competition. Avoidance of inbreeding would also predict that offspring from enlarged broods would disperse further (Greenwood & Harvey 1982). This again stresses that a simple prediction of natal dispersal is difficult to give.

**EVOLUTIONARY ASPECTS**

If the brood size effect on natal dispersal distance is general, and clutch size is heritable, small mutations in clutch size will not only change costs and benefits associated to the clutch of those parents but also affect the spatial scale at which such mutation will spread. Clutch sizes may evolve differently in spatially structured habitats in comparable ways as genes for flight in carabid beetles (Boer 1970). Evolution of clutch size will therefore depend on the meta-population structure. If such effects are important we might expect that immigrants differ from resident birds in that they lay larger clutchs. There is evidence from three populations that this is the case. In the Lauwersmeer population immigrants (birds that were not ringed as a nestling) indeed laid larger clutches in the experimental years (1995, 1997 and 1998, difference: 0.4 eggs, $F_{1,300} = 4.870$, $P < 0.03$, year effect $F_{3,300} = 0.642$, $P > 0.5$). However, as this difference has not persisted in recent years, its generality can be questioned. In the Hoge Veluwe there also was a small difference in clutch size between immigrants and local birds (1973–93, 0.241 eggs more for immigrants, $F_{1,113} = 4.417$, $P < 0.04$, controlled for year, $F_{2,113} = 17.951$, $P < 0.001$). Also for the great tit population of Vlieland immigrants laid larger clutches than local birds (Verhulst 1995). Verhulst’s explanation for this phenomenon was that immigrants in an island population lay larger clutches because they originate from populations with a genetically larger clutch size and were not locally adapted. We can now see that these results could be explained by the finding that offspring from parents with larger clutches disperse more.

**Conclusions**

To estimate fitness consequences of brood size manipulations we cannot rely on local measurements of prospects of the offspring, but have to collect data on how dispersal distance is affected by the manipulation and how decisions on dispersal relate to subsequent survival and reproduction. The spatial and temporal variation in distribution of resources will interact with the clutch size related dispersal distance and may affect the evolution of clutch size in concert with spatial heterogeneity. Whether this is quantitatively important awaits further study.

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**References**

Auk, 115, 920–936.


van der Jeugd, H.P. (2001) Large barnacle goose males can overcome the social cost of natal dispersal. 
Behavioural Ecology, 12, 275–282.


Quarterly Review of Biology, 67, 111–130.


Oikos, 86, 147–151.


PhD thesis, University of Uppsala.


Evolution, 42, 351–362.


Petitfor, R.A. (1993a) Brood-manipulation experiments. I. The number of offspring surviving per nest in Blue Tits (Parus caeruleus). 


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