

Minireviews provides an opportunity to summarize existing knowledge of selected ecological areas, with special emphasis on current topics where rapid and significant advances are occurring. Reviews should be concise and not too wide-ranging. All key references should be cited. A summary is required.

Density-dependent dispersal in birds and mammals

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Density-dependent dispersal can be caused by various mechanisms, from competition inducing individuals to emigrate (positive density-dependence) to social crowding effects impeding free movement (negative density-dependence). Various spatial population models have incorporated positively density-dependent dispersal algorithms, and recent theoretical models have explored the conditions for density-dependent dispersal (DD) to evolve. However, while the existence of DD is well documented in some taxa such as insects, there is no clear picture on its generality in vertebrates. Here I review the available empirical data on DD in birds and mammals, focusing mainly on variation in dispersal between years and on experimental density manipulations. Surprisingly few studies have explicitly focused on DD, and interpretation of the available data is often hampered by differences in approach, small sample sizes and/or statistical shortcomings. Positive DD was reported in 50 and 33% of the selected mammal and bird studies, respectively, while two studies on mammals (out of eight) reported negative DD. Among bird studies, DD was more often reported for emigration rates or long-distance recoveries than for average distances within finite study areas. Experimental studies manipulating densities (mainly on mammals) have consistently generated positive DD, typically showing reduced emigration in response to partial population removal. Studies that examined dispersal in relation to seasonal changes in density (small mammals only) have more often reported negative DD. Studies that compared dispersal between sites differing in density, also show a mixture of positive and negative DD. This suggests that dispersal changes in a more complex way with seasonal and spatial density variation than with annual densities, and/or that these results are confounded by other factors differing between seasons and sites, such as habitat quality. I conclude that both correlational and experimental studies support the existence of positive, rather than negative, density-dependent dispersal in birds and mammals.

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The analysis of density-dependence in demographic processes is crucial to the study of population dynamics. The main emphasis is usually on density-dependence in fecundity and survivorship (Fowler 1981, Murdoch 1994, Wolff 1997, Newton 1998, Saether et al. 2002). More recently, and in conjunction with an increased awareness of the importance of spatial processes in population biology (Hanski and Gilpin 1997, Clobert

et al. 2001), there is a growing realization of the importance of density-dependence in movement rates as well. Increasingly, density-dependent dispersal functions are being implemented in both theoretical and applied population models (e.g. Wu et al. 1993, Scheuring and Janosi 1996, Veit and Lewis 1996, Foppen et al. 2000). Several theoretical studies have stressed the role of density-dependent dispersal (DD) in stabilizing

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population fluctuations in heterogeneous environments (Paradis 1997, Haydon and Steen 1997, Amarasekare 1998, Ruxton and Rohani 1998, Saether et al. 1999, Amarasekare 2004). Other studies have started to explore the conditions that may lead to the evolution of DD as an adaptive strategy (Travis et al. 1999, Poethke and Hovestadt 2002, Cadet et al. 2003) or as an outcome of competitive interactions (McCarthy 1999).

Despite these theoretical developments, the amount and quality of empirical information on DD has not increased at the same pace, and shows a strong taxonomic bias. Recent papers have asserted that there is “much empirical evidence from a wide range of taxa that (...) dispersal rate can both increase and decrease with population density” (Travis and French 2000) and that “density-dependent dispersal (emigration) is common across most taxa considered” (Lambin et al. 2001). While there is clear evidence for widespread DD in some taxa, notably in various insect groups (e.g. Harrison 1980, Denno and Peterson 1995), for other taxa – vertebrates in particular – the evidence is more equivocal. For example, of the three studies cited by Travis and French (2000) to support DD in birds, one study was based on only four years of data (Nilsson 1989), one used reproductive success as a proxy for population density (Veit 1997) and the third reported a relationship between dispersal and post-dispersal densities, rather than pre-dispersal (Greenwood et al. 1979). Other authors have taken a more critical or at least cautionary view: “few studies of birds have shown that dispersal is greatly influenced by population density” (Hines 1986) or “the question of DD in small mammals remains largely unanswered” (Diffendorfer et al. 1999).

In this paper the available evidence for DD in birds and mammals is reviewed for the first time. Birds and mammals are particularly relevant in this respect, because they make up the majority of target species for spatial population viability analysis (PVA) models, where dispersal parameters and/or dispersal rules are a crucial component (e.g. Lindenmayer et al. 2003). DD is virtually unstudied in vertebrates other than birds and mammals (but see Léna et al. 1998, Lecomte et al. 2004). I focus on natal dispersal, defined as the movement between the natal area or social group and the area or social group where first breeding takes place (following Clobert et al. 2001) but I will distinguish between different measures of dispersal, notably emigration rates and distance parameters. I chose not to incorporate studies on immigration rates, since usually there is no information on densities in the sites where immigrants may have originated from. I also did not consider studies using immigration in removal plots (often called recovery rates). This was a popular technique to estimate dispersal in small mammals in the 1970s (Joule and Cameron 1975, Windberg and Keith 1976, Fairbairn

1978, Gaines et al. 1979) but its use has remained controversial (Dobson 1981, Cockburn 1985, Krebs 1992). Boutin et al. (1985) concluded that this method overestimates dispersal in comparison with telemetry data, particularly in high density periods.

The initial focus in this review is on correlative analyses of annual variation in dispersal rates, and on experimental manipulations of density. This leaves out two kinds of data which nevertheless will be more briefly considered in separate sections: studies involving spatial comparisons, and studies comparing dispersal between seasons or even shorter periods within annual cycles. Translating spatial patterns into temporal DD is not straightforward (Newton 1998). The main problem is that observed spatial density patterns are likely to be correlated with differences in habitat quality and/or phenotypic composition, and hence density values in different sites can have very different meanings (Andreassen and Ims 2001). For instance, a low-density site 1) may be temporarily recovering from a population crash and thus represent optimal habitat with a population below carrying capacity, 2) may consist of a mosaic of suitable and unsuitable habitat and therefore have low carrying capacity but good fitness prospects, or 3) may consist of marginal habitat only selected by individuals unable to reproduce elsewhere. In these three scenarios one might predict low, average or high emigration rates for locally born individuals in comparison to high-density sites, even without considering the possibility of condition-dependent dispersal related to habitat quality (Ims and Hjermann 2001). This problem can be extended to studies that did not discriminate between spatial and temporal variation in their statistical analyses (e.g. Forero et al. 2002). The experimental study by Slade and Balph (1974) on ground squirrels illustrates the complex possible interactions between spatial and temporal density-dependence. In this study, experimental reduction of density within a heterogeneous area resulted in a reversal of per capita dispersal rates between subareas: at high (unmanipulated) density more ground squirrels moved from the optimal to the suboptimal part, while the reverse occurred at experimentally lowered densities.

Studies on dispersal in relation to intra-annual changes in density pose analogous problems to studies on spatial variation. Intra-annual changes in density are unavoidably confounded with variation in a number of factors including timing of reproductive events, changes in age composition, general environmental conditions, and – particularly in life-cycles with multiple generations per year – also with phases of population growth and decline. Furthermore, time units are also arbitrarily defined (Krebs 1992) and successive observation periods are not statistically independent. Proper statistical analysis should take these different factors into account, but this is rarely done. A similar problem applies to data

obtained from populations going through multi-annual cycles (see Results). An additional argument for focusing on annual variation in noncyclic populations is that models implying density-dependent dispersal rules – whether theoretical or applied, such as PVA – typically address year-to-year fluctuations and generally do not consider cyclic fluctuations (but see Chapman et al. 2001).

Before discussing the empirical data I will briefly review the main hypotheses that predict the existence of density-dependence in dispersal.

General hypotheses

Positive density-dependence

Probably the most widespread hypothesis on density-dependent dispersal is that competition increases the likelihood of dispersing because individuals have better fitness prospects by leaving high-density sites (Murray 1967, Greenwood and Harvey 1982, Waser 1985, Porter and Dooley 1993). The increase in dispersal may be mediated through dominance interactions or outright aggression (McCarthy 1999), or by deteriorating environmental conditions as a consequence of crowding (Denno and Peterson 1995). Several models have explored the consequences under which positive DD is expected to evolve as an adaptive strategy. Probably the earliest model was published by Gadgil (1971) who predicted strong DD if spatial variation in habitat quality was high. This conclusion was corroborated by several more recent studies (McPeck and Holt 1992, Johst and Brandl 1997, Travis et al. 1999, Metz and Gyllenberg 2001, Poethke and Hovestadt 2002).

McCarthy (1997, 1999) modelled DD as a conditional strategy in the face of constraints on finding a place to settle in competitive conditions, thereby expanding earlier efforts by Murray (1967) and Waser (1985). He predicted that competition would lead to increased dispersal but only up to a point; above a critical ratio of dispersers to vacancies, realized dispersal will decrease again because vacancies are increasingly filled by short-distance dispersers while long-distance dispersers increasingly fail to settle.

A different hypothesis invokes the higher likelihood of females being harassed by males to predict sex-specific positive DD in butterflies or other insects (Baguette et al. 1998). This hypothesis may be less applicable to vertebrates where mating behaviour and its relationship with movement decisions are more complex.

Negative density-dependence

Whereas the previous hypotheses primarily view dispersal as a means to escape from poor conditions and/or

from social interactions, the “social fence” and related hypotheses (Hestbeck 1982, Lambin et al. 2001) predict that high densities actually lead to reduced dispersal (particularly reduced immigration) because of the increasing likelihood of aggressive encounters. The social fence will act more strongly if residents are not only intolerant of new settlers, but also of transient individuals not (yet) attempting to settle. Negative density-dependence can also be caused by conspecific attraction, i.e. a tendency for individuals to be attracted to areas with many conspecifics (Danielson and Gaines 1987, Stamps 1991) or inversely, to emigrate out of low-density areas which may induce local Allee effects (Kuussaari et al. 1998). Conspecific attraction can be explained by the benefits of social aggregations (e.g. anti-predator behaviour, social foraging) or by the use of conspecific density as a cue for availability of resources or mates.

High densities may also favour philopatry if non-dispersing offspring have the option to remain on the natal territory or in the natal group, rather than dispersing in a saturated environment (Jones et al. 1988, Stacey and Ligon 1991, Forero et al. 2002). However, this hypothesis does not apply to species with obligate natal dispersal out of the natal home-range or territory.

Another, rather idiosyncratic mechanism for negative DD was proposed by Stenseth and Swingland (1983) for rodents, suggesting that increased predator abundance during population peaks would reduce disperser survival and hence realized dispersal.

If local densities do not vary in synchrony within the range of dispersers, it is possible that dispersal is affected differently by densities in the natal (or departure) area, and the area of settlement. In principle all hypotheses mentioned above can be applied to densities in both natal and settlement areas, but whether this is true will depend on the actual mechanisms and decision rules involved. For example, the “social fence” effect could act as a one-way filter if residents interact differently with emigrants/transients and with putative settlers. This is a particular problem when data on different phases of the dispersal process are compared, i.e. emigration, transience and immigration (Ims and Yoccoz 1997). This review mainly includes two types of data: emigration from a focal study area where emigrants are scattered over a wider area, and their fates often incompletely known; and dispersal distances inside relatively small study areas where spatial density variation is not reported. Thus, all cases of DD reported are in relation to densities in the area of departure.

Data and analysis

The number of empirical studies focusing mainly or entirely on density-dependence in dispersal is very

limited. An initial Web of Science (ISI) search on papers containing both “density-dependence” and “dispersal” in the title yielded only a handful of relevant papers on birds and mammals. Most information was therefore obtained through an ad lib search among papers focusing more broadly on dispersal and/or population dynamics.

Among the selected papers, there was considerable variation in the nature of the dispersal parameters used. A number of studies had to be excluded because they provided absolute measures of dispersal rate, and per capita rates could not easily be extracted from the paper (e.g. Gaines et al. 1979, Russell and Rowley 1993, Cittadino et al. 1998). Verner and Getz (1985) measured dispersal as the ratio of net emigration events over all passages through an enclosure, which is also difficult to translate into per capita dispersal. Most studies included in the review have used emigration rate (or its complement, local recruitment or philopatry). Emigration has typically been considered in relation to a limited study area but in some cases, dispersal was defined as emigrating out of the natal range (e.g. Wahlström and Liberg 1995, Pasinelli and Walters 2002). Other studies have provided metrics of the dispersal distance distribution (typically averages, sometimes proportion of long-distance recoveries). Several bird studies measured distance in number of territories (Martin and Hannon 1987, Nilsson 1989) rather than physical distance. One study (Greenwood et al. 1979) converted distance into territories based on population densities; because of the obvious circularity involved, I only considered their results on distance per se. In several cases, emigration data were inferred from local disappearance of individuals. These data were only included if it could be reasonably assumed that mortality was negligible or at least insufficient to explain the variation in disappearance rates (Ekman 1984, Watson et al. 1984, Lambin 1994). Finally, four studies used idiosyncratic measures of dispersal. Hanski et al. (1991) used the number of colonists trapped on small islets as a measure of dispersal from the mainland. Three studies on ungulates examined the strength of mother-offspring associations or the ratio of family groups vs solitary individuals as a proxy for philopatry (Albon et al. 1992, L’Heureux et al. 1995, Vincent et al. 1995). Only two studies included in this review have analyzed multiple measures of dispersal (distance and emigration rate) obtained in the same population(s) (Jones et al. 1988, McGuire et al. 1993). Lambin (1994) also reported on both emigration and distances, but not over the same time units.

Since dispersal distance distributions within limited study areas are typically highly censored (Baker et al. 1995) and therefore may be less likely to reveal significant variation, I distinguished between data on local dispersal (i.e. metrics of distance, family associations or proportion dispersing within a confined study area) and

nonlocal dispersal (philopatry/emigration, or metrics of distance based on observations in a wider area, e.g. general ringing data). All statistical analyses reported were performed using SAS 8.2 (procedures CORR, NPAR, FREQ, GENMOD). All tests are two-tailed.

Results

Annual variation: birds

I found 29 studies on birds (27 sources, 22 different species) that reported a relationship between annual population density and dispersal, measured as emigration rate/philopatry, average dispersal distance, or the frequency of long-distance dispersal (Table 1). Different density measures were used in different studies, sometimes several in the same study: density at time of birth, density at time of first breeding (i.e. post-dispersal), juvenile (=first-year bird) density, or density at the time of dispersal i.e. typically late summer or autumn (e.g. Ekman 1984). This variation reflects the typical design of most bird population studies where censuses occur only once per year, while in mammal studies (see further) densities are often determined from capture-recapture sessions that simultaneously yield the dispersal data. The number of years included per study varied from 4 to 36. One study addressed a population going through a multi-annual cycle (Watson et al. 1984).

Among these studies, 13 reported positive density-dependence in dispersal (DD) in one or both sexes, three reported negative DD, and the remaining 13 found no relationship. However, I considered eight studies to provide insufficient support for DD. In seven of these, dispersal changed over time during a period of population in- or decrease, and no attempt was made in the paper to separate the time trend from the density effect (O’Connor 1980, Coulson et al. 1982, Wyllie and Newton 1991, Heinze et al. 1996, Negro et al. 1997, Lindberg et al. 1998, Pyle 2001). Moreover, only two of these studies actually regressed dispersal on annual densities (O’Connor 1980, Pyle 2001) while the others compared dispersal between longer time periods e.g. with low and high population sizes. Two other studies also dealt with population trends (Winkel and Frantzen 1989) but inspection of the data strongly suggests that the density effect was not confounded by the time trend, hence these data were kept in the analysis. The eighth study was seriously affected by pseudoreplication because multiple observations within each year were treated as fully independent data, while the number of years was very small (only four) and one single year greatly appeared to affect the outcome (Fig. 3 in Nilsson 1989). In addition, one study reported a negative relationship between dispersal and breeding (i.e. post-dispersal) density but not with natal density (Greenwood et al. 1979); for this

Table 1. Studies on density-dependent dispersal in birds, based on annual variation. Density-dependence: no/pos/neg = no, positive or negative relationship reported; pos(F) = positive in females only. Note that "positive" always means an increase in dispersal with density, e.g. an increase in emigration or a decrease in philopatry. Entries in parentheses imply that the reported relationship is not fully substantiated by the data (see text). * indicates local dispersal (i.e. only movements within a confined area are considered). Ny = number of years in analysis. Parentheses for this column indicate that density-dependence was inferred from comparisons between periods rather than individual years. ND = natal density (year of birth), BD = breeding density (year of first breeding), JD = juvenile density at time of dispersal, AD = autumn density. Effect sizes (see also Fig. 1): p = calculated on pooled data across sexes, a = average of sex-specific effect sizes.

Author	species	density-dependence	dispersal parameter	Ny	density parameter	effect size (r)
Heinze et al. 1996	black-headed gull <i>Larus ridibundus</i>	(neg)	philopatry	(36)	ND	
Pyle 2001	cassin's auklet <i>Ptychoramphus aleuticus</i>	(neg)	distance	19	ND	
Lindberg et al. 1998	black brant <i>Branta bernicla</i>	(pos (F))	philopatry	(6)	ND	
Wyllie and Newton 1991	sparrowhawk <i>Accipiter nisus</i>	(pos(F))	dist > 10 km	(10)	ND	
Coulson et al. 1982	herring gull <i>Larus argentatus</i>	(pos)	philopatry	(10)	ND	
Negro et al. 1997	lesser kestrel <i>Falco naumanni</i>	(pos)	philopatry	7	ND	
Nilsson 1989	marsh tit <i>Parus palustris</i>	(pos)	dist(terr)*	4	JD	
O'Connor 1980	great tit <i>Parus major</i>	(pos)	dist > 10 km	16	ND	
Greenwood et al. 1979	great tit <i>Parus major</i>	neg (F)/no	distance*	12	BD/ND	-0.09 (a)
Altwegg et al. 2003	barn owl <i>Tyto alba</i>	no	emigration	11	ND	
Arcese 1989	song sparrow <i>Melospiza melodia</i>	no	distance*	5	ND	-0.39 (a)
Hines 1986	blue grouse <i>Dendragapus obscurus</i>	no	distance*	4	BD, JD	0.21 (a)
Keppie and Towers 1992	spruce grouse <i>Dendragapus canadensis</i>	no	emigration	11	AD	
Marti 1999	barn owl <i>Tyto alba</i>	no	distance	18	JD	-0.01 (p)
Martin and Hannon 1987	willow ptarmigan <i>Lagopus lagopus</i>	no	dist(terr)*	4	ND	
Matthysen et al. unpubl.	blue tit <i>Parus major</i>	no	distance*	9	ND	-0.61 (p)
Matthysen et al. unpubl.	great tit <i>Parus major</i>	no	distance*	9	ND	0.30 (p)
Newton and Marquiss 1983	sparrowhawk <i>Accipiter nisus</i>	no	distance	10	ND, AD, BD	0.15 (a)
Pärt 1990	collared flycatcher <i>Ficedula albicollis</i>	no	distance*	7	ND, BD	-0.14 (a)
van Balen and Hage 1989	blue tit <i>Parus caeruleus</i>	no	dist > 15 km	30	ND	
Wheelwright and Mauck 1998	savannah sparrow <i>Passerculus sandwichensis</i>	no	distance*	8	ND, BD	
Winkel and Frantzen 1989	great tit <i>Parus major</i>	no	dist > 5 km	23	ND	0.08 (p)
Ekman 1984	willow tit <i>Parus montanus</i>	pos	emigration	6	JD	
Moss and Oswald 1985	capercaillie <i>Tetrao urogallus</i>	pos	emigration	9	JD	
van Balen and Hage 1989	great tit <i>Parus major</i>	pos	dist > 15 km	30	ND	
Winkel 1989	nuthatch <i>Sitta europaea</i>	pos	dist > 5 km	32	ND	0.51 (p)
Winkel and Frantzen 1991	blue tit <i>Parus caeruleus</i>	pos ¹	dist > 5 km	29	ND	0.44 (p)
Watson et al. 1984	red grouse <i>Lagopus l. scotica</i>	pos	emigration	14	ND	
Nager et al. 1996	greater flamingo <i>Phoenicopterus ruber</i>	pos	emigration	5	JD	

¹Inspection of Figs 1 and 5 shows that the time trend in density is insufficient to explain DD.

study I only considered the relationship with natal density which was not significant.

This reduces the number of cases reporting positive, negative or no DD to 7, 0 and 14, respectively (Fig. 1). The predominance of positive over negative signs (7/7) is statistically significant (binomial test, $p=0.02$). DD was reported more often for nonlocal (7 of 13 studies) than for local dispersal (0 out of 8) (Fisher exact test, $p=0.02$). Among the seven studies excluded because of the confounding time trend, five had positive and two negative trends (Table 1).

Table 1 shows that the number of years of data analyzed is often short, in some cases only 4 or 5 yr (median = 10; $n=21$). With the exception of five studies (six entries) using general ringing recovery data (van Balen 1980, Winkel 1989, Winkel and Frantzen 1989, 1991, Marti 1999), no studies have included >14 yr. Studies on nonlocal dispersal included more years than studies on local dispersal (median: 14 vs 7.5, $n=13$ and 8; Kruskal-Wallis test, $\chi^2=7.0$, $p<0.01$). However, there was no significant difference in the number of years between studies that did or did not report DD (median: 14 and 14.5, $n=7$ and 14; Kruskal-Wallis test, $\chi^2=1.1$, $p=0.3$) and the higher occurrence of positive results in nonlocal dispersal (see previous paragraph) was not affected by study duration (logistic regression; details not shown).

A full meta-analysis on these results was not possible because many studies did not provide detailed statistics, and some provided separate analyses per sex while others pooled the sexes. Nevertheless I extracted effect sizes (correlation coefficients) for pooled sexes from seven studies, and sex-specific effect sizes for five other studies which I then averaged. The mean effect size for nonlocal dispersal was close to being significantly different from

zero (mean $r=0.29$, $p=0.08$, $n=7$) and also tended to be higher than the mean for local dispersal ($t_{10}=-1.9$, $p=0.086$) which in itself did not differ from zero (mean $r=-0.13$, $p=0.5$, $n=5$). A graph of effect sizes versus study duration (Fig. 2) shows no indication of a linear trend with study duration, but a reasonable resemblance to the expected funnel-shaped graph with higher sampling variance in smaller samples. Thus, there is no immediate reason to suspect publication bias (Møller and Jennions 2001).

Annual variation: mammals

I found 16 studies on mammals (15 sources, 14 different species) where dispersal parameters could be related to annual variation in density (Table 2). One experimental comparison is not included here (see next paragraph: Slade and Balph 1974). Most studies reported emigration data (8), six reported distances or proportions dispersed inside the area (one provided emigration data as well), and three used mother-offspring or family associations as a proxy for philopatry. There were comparable numbers of studies reporting positive DD, negative DD or none, i.e. five, six and five respectively (but see footnote 4 to Table 2). However, four studies involved substantial time trends in population size which made it impossible to separate time trends from density effects (cf. supra) (Berger 1987, Wahlström and Liberg 1995, L'Heureux et al. 1995) and four studies (three sources) addressed a time period that included less than a full cycle from a multi-annual population cycle (Boutin et al. 1985, Rodgers 1990, Lambin 1994). Moreover, several of these studies did not explicitly test the relationship with density, but compared pre-defined

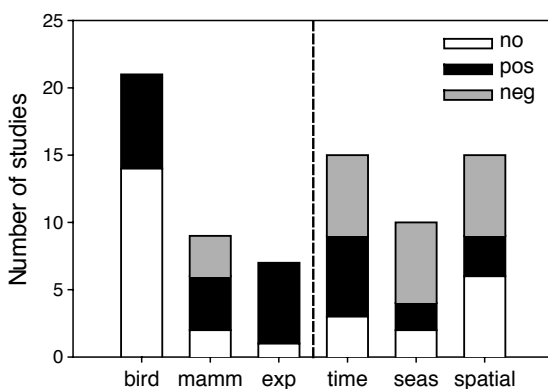


Fig. 1. Frequency of studies reporting no, positive or negative density-dependent dispersal, grouped in six categories. From left to right: studies on annual variation in birds and mammals; experimental manipulations of density (6 mammals, 1 birds); studies on annual variation confounded by time trends in population size (7 birds, 8 mammals); studies on intra-annual variation (mammals only); and studies on spatial variation in density (5 birds, 10 mammals).

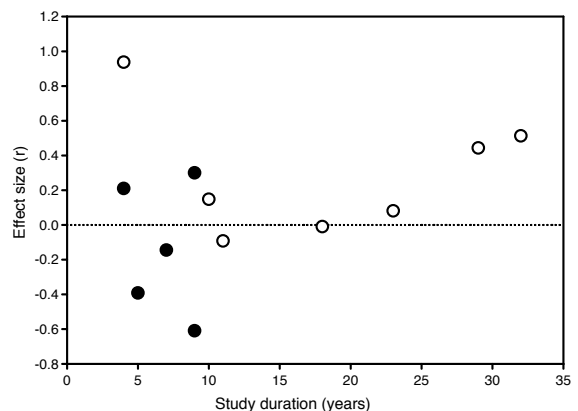


Fig. 2. Graph of effect size (correlation between population density and dispersal) versus study duration, for eleven studies on birds where correlation coefficients could be extracted. Black symbols = "local" dispersal (average distance within a confined study area), white symbols = "non-local" dispersal (emigration or distances within larger study areas; see text). For details of the studies involved, see Table 1.

Table 2. Studies on density-dependent dispersal in mammals, based on annual variation. Legend as in Table 1. M-O association = mother-offspring association.

Author	species	density-dependence	dispersal parameter	Ny
L'Heureux et al. 1995	bighorn sheep <i>Ovis canadensis</i>	(neg)	M-O association*	(10)
Wahlström and Liberg 1995	roe deer <i>Capreolus capreolus</i>	(neg)	emigration	(6) ¹
Vincent et al. 1995	roe deer <i>Capreolus capreolus</i>	(neg)	family groups*	(7)
Lambin 1994	Townsend's vole <i>Microtus townsendii</i>	(neg)	distance	3 ²
Boutin et al. 1985	snowshoe hare <i>Lepus americanus</i>	(no)	emigration	4 ³
Rodgers 1990	brown lemming <i>Lemmus sibiricus</i>	(no)	distance*	4
Rodgers 1990	collared lemming <i>Dicrostonyx groenlandicus</i>	(no)	distance*	4
Berger 1987	wild horse <i>Equus caballus</i>	(pos)	distance*	5
Jones et al. 1988	banner-tailed kangaroo rat <i>Dipodomys spectabilis</i>	neg	distance*, emigration	(7)
Berry and Jakobson 1974	house mouse <i>Mus musculus</i>	neg(F) ⁴	proportion dispersing*	5
Hanski et al. 1991	common shrew <i>Sorex araneus</i>	no ⁵	emigration	5
Gese and Mech 1991	grey wolf <i>Canis lupus</i>	no	emigration	(20)
Barash 1973	Olympic marmot <i>Marmota olympus</i>	pos	emigration	3
Albon et al. 1992	red deer <i>Cervus elaphus</i>	pos	M-O association*	10
Wauters et al. 2004	red squirrel <i>Sciurus vulgaris</i>	pos	emigration	19 ⁶
Catchpole et al. 2004	red deer <i>Cervus elaphus</i>	pos ⁷	emigration	24

¹two areas with 6 yr each.

²one high-density year compared with two low-density years.

³no formal test on association with density.

⁴calculated from their Tables I and II, i.e. proportion spring-to-summer dispersers related to spring density.

⁵contra authors: reanalysis shows nonsignificant correlation ($r = 0.58$, $P = 0.3$) between per capita dispersal and population size.

⁶two areas with 9 and 10 yr each.

⁷relationship decreases with higher values of North Atlantic Oscillation; positive relationship contradicts an earlier study (Clutton-Brock et al. 1982).

periods within the population cycle or trend (Boutin et al. 1985, Rodgers 1990, Wahlström and Liberg 1995) and/or addressed few years (Lambin 1994). Of these eight studies, four showed negative, one positive, and three no DD.

Among the remaining eight studies, I found two negative (one of them sex-specific) and four positive cases of DD, and two studies without DD (Fig. 1). The proportion of studies with positive DD is somewhat larger than in birds but not significantly so ($4/8 = 50\%$; $7/21 = 33\%$; Fisher exact $p = 0.4$). Considering only non-local dispersal the difference reverses but is also non-significant ($2/6$ vs $7/13$; Fisher exact $p = 0.6$). The number of years per study is also comparable to birds (3–24, median = 8.5 yr). No attempt was made to further analyse effect sizes, given the small number of studies ($n = 8$) remaining and the fact that not all reported statistical details.

Experimental data

A small number of studies have manipulated local densities to study dispersal behaviour of the remaining individuals or of introduced animals (Table 3). Two studies compared experimental and control years within the same area (Slade and Balph 1974, Brody and Armitage 1985) while five others compared control and removal sites. The six studies on mammals all found positive DD, i.e. lower emigration in response to

removals (binomial test, $p = 0.03$). These include two cases where the response was only found in females. The single study on birds reported no effect, bringing the total to six positive out of seven studies (Fig. 1).

Combining the experimental data with the previously discussed studies on annual variation (Tables 2, 3), we see that the majority of studies on mammals found positive DD (10/14) and positive signs predominate over negative signs (10/12; binomial test, $p = 0.04$). The latter is not different from the situation in birds (7/7; Fisher exact test, $p = 0.5$). Pooling all studies (correlative/experimental, birds and mammals) the number of studies with positive, negative or no DD is 17, 2 and 17, respectively (47%, 6%, 47%) (see also Fig. 1).

In the next two paragraphs I will briefly review two additional sets of studies which I consider to constitute weaker tests of density-dependence in dispersal for reasons explained in the introduction, i.e. studies on intra-annual variation, and spatial comparisons.

Intra-annual variation

Table 4 lists ten studies that analyzed per capita emigration and/or dispersal distance in relation to intra-annual density changes, all on small rodents (7 species; see introduction for reasons why many other dispersal studies on rodents were not included). Units of time periods varied from weeks to several months. One study not included is worth mentioning here: Diffendor-

Table 3. Experimental studies on spatial density-dependence in dispersal in birds and mammals. All studies used emigration as dispersal parameters except Loew (1999, distance).

Author	species	density-dependence	N
Keppie and Towers 1992	spruce grouse <i>Dendragapus canadensis</i>	no	4 sites
Danielson and Gaines 1987	prairie vole <i>Microtus ochrogaster</i>	pos ¹	20 sites
Loew 1999	eastern chipmunk <i>Tamias striatus</i>	pos	2 sites
Brody and Armitage 1985	yellow-bellied marmot <i>Marmota flaviventris</i>	pos (F)	3 sites ²
Davis et al. 1964	woodchuck <i>Marmota monax</i>	pos	2 sites
Slade and Balph 1974	Uinta ground squirrel <i>Spermophilus armatus</i>	pos	2 periods
Aars and Ims 2000	tundra vole <i>Microtus oeconomus</i>	pos (F)	12 sites

¹emigration of individuals introduced in removal plots.

²one removal site was compared with pre-removal years as control.

fer et al. (1999) reported negative temporal DD for several species, but they apparently did not include observations with zero dispersers in their analysis on log-transformed proportions. Since zeroes are more likely to occur when overall numbers of animals are low, this creates a bias towards negative DD, as can be seen from their graphs. Several of the studies in Table 4 have not formally tested the association between density and dispersal (DeLong 1967, Beacham 1980), and none of the studies provide a way to separate density effects from other effects associated with time periods or seasons, including the increase or decrease in numbers. Six studies showed negative DD, two positive, and two none – with three studies showing an effect in one sex only (Fig. 1). The ratio of negative over positive signs (6 vs 2) is not significantly different from the ratio among studies on annual variation in mammals (2 vs 4; Fisher exact $p=0.27$) but differs from the overall ratio among other mammal studies, including experimental ones (2 vs 10; Fisher exact $p=0.02$).

Spatial comparisons

Table 5 lists 15 studies where dispersal distances or emigration rates were examined in relation to spatial variation in density (5 birds, 10 mammals). This list is probably not exhaustive; for example, no attempt was

made to include independently published estimates from different populations for the same species. Sample sizes varied widely, from only two patches or populations to 56, as did the spatial scales involved (from adjacent patches within study areas to geographically distinct populations or colonies). Three studies regressed individual dispersal on local population densities. However, four studies, including the latter three, did not separate spatial and temporal variation in population densities. Among the fifteen studies, six found no DD, six negative DD, and only three positive DD (Fig. 1). This distribution is significantly different from the results obtained from bird and mammal studies combined (including experimental data, see above; Fisher exact $p=0.01$). The proportion of negative signs among studies reporting DD is also higher (6/9 vs 2/19; Fisher exact $p=0.005$).

Discussion

In this review I focused mainly on density-dependence in dispersal (DD) in birds and mammals as shown by annual variation in mean dispersal distance or emigration, and by experimental density manipulations. As argued in the introduction, these data provide the most straightforward test on how dispersal rates change with population density. A first and rather general conclusion from this review is that the number of informative

Table 4. Studies where dispersal was evaluated in relation to intra-annual changes in density. Legend as in Table 1. N = sample size.

Author	species	density-dependence	dispersal parameter	N
Rehmeier et al. 2004	deer mouse <i>Peromyscus maniculatus</i>	neg	emigration	20 seasons
McGuire et al. 1993	prairie vole <i>Microtus ochrogaster</i>	neg	emigration, distance	(7 yr) ¹
Lin and Batzli 2001	prairie vole <i>Microtus ochrogaster</i>	neg	emigration	8 periods × 4 areas
Lin and Batzli 2001	meadow vole <i>Microtus pennsylvanicus</i>	neg	emigration	8 periods × 4 areas
Boonstra 1989	meadow vole <i>Microtus pennsylvanicus</i>	neg (F) ²	distance*	7 seasons
Sandell et al. 1990	field vole <i>Microtus agrestis</i>	neg (M)	distance*	(2 yr) ³
Tattersall et al. 2004	wood mouse <i>Apodemus sylvaticus</i>	no	emigration	24 months
Beacham 1980	Townsend's vole <i>Microtus townsendii</i>	no	emigration	8 seasons × 2 areas
DeLong 1967	house mouse <i>Mus musculus</i>	pos	proportion dispersing*	6 months (2 areas)
Lambin 1994	Townsend's vole <i>Microtus townsendii</i>	pos (F)	emigration	24 months

¹trapping periods were assigned to either high or low density.

²only for females maturing in the year of birth.

³individuals were used as unit for statistical analysis.

Table 5. Studies where dispersal was compared between sites with different population densities. Legend as in Table 1. N = sample size (note that “patches” refers to spatial units within a study population, “populations” to study sites separated by larger distances). The last column indicates whether studies combined spatial and temporal variation in their analysis.

Author	species	density-dependence	dispersal parameter	N	spatial + temporal
Forero et al. 2002	black kite <i>Milvus migrans</i>	neg	distance	285 individuals	
Jones et al. 1988	banner-tailed kangaroo rat <i>Dipodomys spectabilis</i>	neg	distance*, emigration	2 populations	x
Andreassen and Ims 2001	root vole <i>Microtus oeconomus</i>	neg	emigration	56 patches	x
Lin and Batzli 2001	prairie vole <i>Microtus ochrogaster</i>	neg	emigration	16 patches	
Lin and Batzli 2001	meadow vole <i>Microtus pennsylvanicus</i>	neg	emigration	16 patches	
Woodroffe et al. 1993	european badger <i>Meles meles</i>	neg	emigration	4 populations	
Payne 1991	indigo bunting <i>Passerina cyanea</i>	no	distance*	2 populations	
Aebischer 1995	shag <i>Phalacrocorax aristotelis</i>	no	emigration	5 colonies	
Pasinelli and Walters 2002	red-cockaded woodpecker <i>Picooides borealis</i>	no	emigration	1281 individuals	x
Wahlström and Liberg 1995	roe deer <i>Capreolus capreolus</i>	no	emigration	76 individuals	
Loison et al. 1999	chamois <i>Rupicapra rupicapra</i>	no	emigration	2 populations	
Fasola et al. 2002	little egret <i>Egretta garzetta</i>	no	emigration	537 individuals	x
Bunnell and Harestad 1983	black-tailed deer <i>Odocoileus hemionus</i>	pos	distance*	2 populations	
Trewhella et al. 1988	red fox <i>Vulpes vulpes</i>	pos	distance*	10 populations	
Ferreras et al. 2004	Iberian lynx <i>Lynx pardinus</i>	pos	emigration	2 populations	

studies appears to be extremely limited, compared to for instance studies on phenotypic correlates of dispersal (various chapters in Clobert et al. 2001) or on sex-biased dispersal in birds and mammals (reviewed by, among others, Clarke and Saether 1997). I suggest that this signals a lack of scientific interest rather than a lack of data, based on the following observations: 1) very few of the available studies actually had density-dependent dispersal as the main topic; 2) a disproportionately large fraction of studies was found in the older (pre-1990) literature; 3) several papers are based on population studies that were continued for many more years after publication, but no reanalyses have been published (e.g. Greenwood et al. 1979, Newton and Marquiss 1983, Arcese 1989, Pärt 1990). This lack of follow-up or valorisation of accumulating data can be attributed either to a change of research priorities since the 1970s–1980s when the discussion on population regulation by dispersal was at its peak, and/or a publication bias (Møller and Jennions 2001) disfavouring the publication of new analyses of the same questions with additional data. On the positive side, the fact that most data were found in papers addressing more general questions of population regulation and/or dispersal, suggests that the publication bias with respect to the actual results should be minimal, because it is unlikely that the outcome on DD determined whether or not the data were published. The recently renewed interest in DD (see Introduction) has not yet provided an increase in empirical data based on longer time series. Some recent studies have been published based on large datasets, but without distinguishing between spatial

and temporal variation in densities (Pasinelli and Walters 2002, Forero et al. 2002). Another recent study (Catchpole et al. 2004) analyzed dispersal jointly with survival in a long-term dataset but without any biological interpretation.

Another general conclusion is that the quality of the published results is often rather poor, both in terms of sample sizes (number of years or sites) and statistical analysis. For instance, several studies have pooled high- and low-density years without explicit justification, raw data are not always provided, and statistical analyses are often outdated. In particular, no study has explicitly addressed the problem of nonindependence of observations in successive time periods. The diversity of parameters and approaches used (years pooled or not, sexes pooled or not) further prohibited the application of a full meta-analysis. Nevertheless, a partial analysis on mean effect sizes in birds confirmed the general trend, and showed no obvious publication bias.

A particular problem was posed by datasets with significant time trends in population size, including a few with data from a limited period within a multi-annual cycle. Only one study made a serious attempt to statistically separate time trends and density effects (van Balen and Hage 1989). In a few cases it appeared as if the population trend was the main reason for reporting DD in the first place (e.g. Wyllie and Newton 1991, Heinze et al. 1996). It is remarkable that most of these studies involving trends in population sizes reported significant DD (12/15), which is close to being statistically different from studies on annual variation in stable populations (13/29; Fisher exact $p=0.052$; see

also Fig. 1). Several explanations can be suggested for this, both biologically and methodologically. First, dispersal may have been correlated with the population trend or an environmental covariate associated with the trend, rather than with density itself. Second, statistical effects may have been inflated by nonindependence of consecutive years' data, e.g. by runs of years with large populations as well as with environmental conditions facilitating dispersal. Third, there may be a stronger publication bias in studies on dispersal in growing or shrinking populations. This would imply that authors are more inclined to publish, and/or editors more likely to accept, results on DD in nonstable populations if there is a significant pattern, compared to results showing no such relationship.

Notwithstanding the weakness of some studies, the general pattern that emerges is that density-dependent dispersal is fairly common in birds and mammals (nearly half of all studies) and predominantly positive. This is in agreement with most evolutionary models that predict an increase in dispersal because of competitive interactions at high densities, and suggests that conspecific attraction and/or social fence mechanisms are much less common. It also supports the general application of positive density functions (either linear or threshold) in various spatial population models. Only two studies on mammals, both on annual variation, showed negative DD (in one case sex-specific) (Berry and Jakobson 1974, Jones et al. 1988), but both were also based on a small number of years. Jones et al. (1988) attributed this result to benefits of philopatry in a saturated habitat, while Berry and Jakobson (1974) did not discuss their result further. Bird studies at first sight appear to show less DD than mammal studies (Fig. 1), but this can be explained by the larger number of studies on local dispersal where DD is rarely documented, and the near absence of experimental studies. Local dispersal observations are inevitably highly censored (Baker et al. 1995, Koenig et al. 1996), and probably result in a lower power of detecting changes in dispersal distribution compared to nonlocal measures such as emigration rate or distances obtained from general ringing recoveries.

Moving beyond density as an explanatory factor for year variation, it is notable that few studies have investigated temporal variation in dispersal rates as such, or searched for factors other than population size that influence annual variation. A notable exception is a number of studies on raptors showing longer dispersal distances in years with low food supplies (Houston and Francis 1995, Adriaensen et al. 1998). This result – although beyond the scope of this review – also supports the notion that increased competition for resources promotes dispersal. Only one study investigated possible interactions between density effects and other factors the interaction between effects (Catchpole et al. 2004, see footnote to Table 2).

For comparison I also reviewed data on seasonal or even intra-seasonal variation in dispersal rates, and on spatial comparisons of dispersal in relation to density. These data were not explored in the same depth for reasons explained in the introduction. Notwithstanding the extensive literature on dispersal in rodents, particularly in relation to population cycles, still relatively few data were found on per capita dispersal rates or measures of dispersal distance. These showed a higher occurrence of negative DD compared to studies on annual variation (Fig. 1), suggesting that changes in dispersal throughout the demographic cycle are associated in a more complex way with population densities than is the case for annual variation, and/or that changes or not only driven by densities but also by other seasonally varying factors. In order to investigate the latter possibility, data will be required from a larger set of seasons/time periods, and a more rigorous statistical analysis that includes not only density levels but also changes in density and other temporally varying factors. The occurrence of negative DD is in agreement with the "social fence" and related hypotheses which have been proposed in particular for small mammal populations, where movements are increasingly inhibited by aggression at high densities (Hestbeck 1982, Stenseth 1988). Other studies, however, did find evidence for positive DD (DeLong 1967, Lambin 1994) and some have claimed that dispersal rates are associated with phases of the population cycle rather than numbers per se (Beacham 1980, Gaines and McClenaghan 1980, Stenseth and Swingland 1983, Rodgers 1990). Obviously, the complex relationships between densities, population growth, social behaviour and dispersal in cyclic populations are yet to be resolved (Stenseth and Lidicker 1992, Lambin et al. 1998, Ims and Andreassen 2000).

Studies on spatial variation also provided a mixed picture with few cases of positive and several with negative DD (Fig. 1). This is in contrast with the experimental studies which only showed positive DD, even though most of them were also based on spatial comparisons. A likely explanation is that spatial variation in density is often related to intrinsic habitat differences, and therefore cannot be easily translated into different levels of crowding or resource competition. Hence, spatial differences cannot easily be extrapolated to changes in dispersal associated with year-to-year fluctuations. It should also be noted that about half of the studies provided data on five sites or less, and often the link with density was based on the existence of significant variation among sites, rather than a significant association with density per se.

In conclusion, positive density-dependence in dispersal appears to be fairly common in studies on annual dispersal rates in birds and mammals, but largely restricted to studies documenting emigration or at least long-distance dispersal events. Experimental manipula-

tions of density, though few, have confirmed this pattern. This conclusion is based on a fairly restrictive set of studies, and apparently a different conclusion could have been drawn if I had not decided to exclude cases with time trends in density, spatial comparisons, and studies on seasonal variation. Obviously there is a need for more studies testing the existence of DD with a more critical approach. First of all there is a need for rigorous statistical analysis of the existing long-term datasets, with appropriate techniques that take temporal (or spatial) autocorrelation into account, and that allow to separate variation in population densities from population growth. Secondly, studies on DD should consider multiple parameters of dispersal that capture variation in the dispersal process at different scales. For instance, bird studies reviewed in this paper provide good evidence for more emigration and/or long-distance movements at high densities, but this has typically not been detected by considering local movements only. This also implies that one should not only look for changes in the mean but also the shape of the dispersal distance distribution, e.g. by considering more complex statistical distributions (see e.g. Tufto et al. in press). The use of immigration rate to study density-dependence remains dubious if densities in the source areas are unknown, which is usually the case. Nevertheless, it can be useful in spatial comparisons if one can assume that all immigrants originate from a common pool, for instance when distances between patches are small compared to the dispersal range of the species (e.g. Matthysen et al. 2001). Finally, correlational analyses should be complemented with experimental density manipulations to test the causality of the observed relationships. Few experiments have been designed to explicitly measure density-dependent dispersal, and even fewer have been carried out in controlled conditions such as field enclosures (Table 3, see also Léna et al. 1998). Experiments in enclosures are particularly useful because they allow to separate dispersal behaviour from realized dispersal, i.e. they take into account differential success of dispersers in relation to density. The latter remains a very difficult task in free-living populations except in those cases where the fate of all dispersers is known; a rare example is provided by Catchpole et al. (2004).

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