Is dispersal distance of birds proportional to territory size?

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Abstract: Recent research has demonstrated that dispersal distance and the square root of home-range size covary proportionately across mammal species. I tested whether these findings could be generalized to another taxon. Breeding territories of some bird species are analogous to mammalian home ranges, so I tested whether dispersal distance and territory size in these birds covaried and were proportional. Variables were $\log_{10}$-transformed before analysis. When considered independently of body mass, median natal dispersal distance and breeding territory size were positively related ($F_{[1,29]} = 8.91$, $R^2 = 0.23$, $P = 0.005$). Median dispersal distance was proportionally related to the square root of territory size by a multiple of 12. This relationship was especially strong for non-migrants ($F_{[1,15]} = 49.84$, $R^2 = 0.77$, $P = 3.87 \times 10^{-6}$). Maximum natal dispersal distance and breeding territory size also covaried when body size effects were removed, but this relationship was only significant when migrants were removed from the sample ($F_{[1,24]} = 5.66$, $R^2 = 0.19$, $P = 0.025$). Maximum dispersal distance did not have a proportional relationship with territory size. This could result from sampling error or from real processes (e.g., relatively shorter dispersals by birds with large territories). The proportional relationship between median dispersal distance and territory size can be used as a cross-species scaling rule.

Résumé : Les résultats de recherches récentes ont démontré que la distance parcourue pendant la dispersion et la racine carrée de la taille de l'aire vitale sont en co-variation proportionnelle chez tous les mammifères. J'ai tenté de déterminer si cela se vérifie chez un autre taxon. Les territoires de reproduction de certaines espèces d'oiseaux sont analogues à des aires vitales de mammifères, alors j'ai essayé de voir si la distance de dispersion et la taille des territoires sont en co-variation et si elles sont proportionnelles. Les variables ont subi une transformation logarithmique ($\log_{10}$) avant d'être analysées. Considérées indépendamment de la taille du corps, la distance médiane parcourue pendant la dispersion à partir du nid et la taille du territoire de reproduction sont en corrélation positive ($F_{[1,29]} = 8{,}91$, $R^2 = 0{,}23$, $P = 0{,}005$). La distance médiane de dispersion est proportionnelle à la racine carrée de la taille du territoire par un multiple de 12. Cette relation est particulièrement forte dans le cas des oiseaux non migrateurs ($F_{[1,15]} = 49{,}84$, $R^2 = 0{,}77$, $P = 3{,}87 \times 10^{-6}$). La distance de dispersion maximale et la taille du territoire de reproduction sont également en co-variation, une fois les effets de la taille du corps annulés, mais cette relation n'est significative que lorsque les oiseaux migrateurs sont retirés de l'échantillon ($F_{[1,24]} = 5{,}66$, $R^2 = 0{,}19$, $P = 0{,}025$). La distance de dispersion maximale n'est pas proportionnelle à la taille du territoire, peut-être à cause d'erreurs d'échantillonnage ou à cause des processus réels (e.g., une distance de dispersion moins importante chez les oiseaux à grands territoires). La relation proportionnelle entre la distance médiane de dispersion et la taille du territoire peut servir de règle de mise en échelle pour l'ensemble des espèces.

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Introduction

Dispersal is an important component of population ecology, yet because it is difficult to measure, dispersal has remained poorly understood (Peles et al. 1999). Bowman et al. (2002) recently demonstrated that dispersal distance in mammals is proportional to the square root of home-range area. They further demonstrated that for mammals, home-range size is a better predictor of dispersal distance than is body mass. Bowman et al. (2002) argued that behaviour and physiology affect the vagility of mammals independently of body mass, such that these two indices of movement (dispersal distance and home-range size) covary proportionately. Thus, mammals with large home ranges (for a given body mass) also will disperse a longer distance than we would expect based on body mass alone. A proportional relationship between dispersal and home-range movements has biological significance. One possible implication is that behavioural and physiological processes have similar effects on both types of movement. Perhaps, for some purposes, we can model these two processes (dispersal and home-range travel) as one larger process called "movement".

A logical extension of this research on mammals is to test whether the results can be generalized to other taxa. In particular, I was interested in the general hypothesis that the extent of different types of space use (e.g., dispersal, home range) covary across species. It has previously been demonstrated that for birds, territory size (Schoener 1968) and dispersal distance (Sutherland et al. 2000) both have positive, allometric relationships with body mass. Bigger birds have larger terri-

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tory sizes and longer dispersal distances than smaller birds. If territory size in birds is similar to home-range size in mammals, relationships among territory size, dispersal distance, and body mass can be compared across bird species. My objective was to test whether the results of Bowman et al. (2002) could be generalized to a taxon other than mammals. I predicted that dispersal distance and territory size in birds should have a positive, proportional relationship when considered independently of body mass. Such a relationship would result if behavioural or physiological characteristics of a given species (e.g., body shape, diet) had similar effects on both dispersal movements and within-territory movements. For example, a long, soft tail can increase the cost of flying (Norberg 1995). The variation among species in movement ability that is caused by such effects on behaviour and physiology often is called “vagility”.

It is possible that bird dispersal distance is not related to species vagility but is instead a function of the distribution of vacant territories. This alternative hypothesis would produce a positive, proportional relationship between dispersal distance and territory size if there is a predictable distribution of vacant territories within any given population; if on average, the *i*th territory from any natal territory is the closest vacant one. This explanation also assumes that any given population’s territories are contiguous, except for exploitable vacancies, and similar in size.

Materials and methods

I used data from Sutherland et al. (2000) for median and maximum natal dispersal distances (km). Birds in their data set served as the pool of species for which I obtained, from published sources, information on territory size (ha). For >90% of species, territory size and dispersal distance estimates were made on separate populations by different investigators. Body mass data (kg) were obtained from Dunning (1993).

Breeding territory size is partly dependent on the feeding strategy of the bird (e.g., Hinde 1956). Some birds feed entirely within their territory, some birds defend only a nest site and feed completely off territory. I was seeking situations that were analogous to mammalian home ranges; thus, only species that feed primarily within their breeding territory were selected. For some species, seasonal home ranges were reported rather than breeding territories. In these cases, home-range size during the breeding period was used as a measure of territory size. Migratory status was recorded but was not a criterion of selection. This process resulted in 50 species for which I had maximum dispersal distance, feeding territory size, and body mass and 31 species for which I had median dispersal distance, feeding territory size, and body mass. Territory sizes and literature sources of these species are listed in Table 1.

I used least-squares regression to relate $\log_{10}$-transformed variables according to the power-law equation:

$$[1] \qquad Y = a \cdot X^b$$

where Y is a response variable; X is an independent variable; a is a scaling constant derived from the regression intercept, but correcting for different units of measure; and b is a constant equal to the regression slope.

The positive, allometric, log-linear relationship between bird territory size (Y in eq. 1) and body mass (X) was demonstrated by Schoener (1968). However, an appropriate standard of comparison was required for my study, and so I reanalyzed this relationship using the territory and body masses that were gathered from my literature review. Then, for each of the median and maximum dispersal distance data sets, I regressed dispersal distance against residuals of body mass. Next, I regressed dispersal distance against territory size. Multiple linear regressions were then used to partition the variance in dispersal distance that could be uniquely explained by territory size and body mass. To further assess effects of body mass, I regressed residuals of the $\log_{10}$ (dispersal distance) vs. $\log_{10}$ (body mass) regressions against residuals of the $\log_{10}$ (territory size) vs. $\log_{10}$ (body mass) regression. Finally, to assess effects of migratory status, these steps were repeated for migrant and non-migrant subsets of the data. Sex-specific analyses were not carried out, as this would have necessitated data splitting and produced small sample sizes. Sutherland et al. (2000) have demonstrated that dispersal distributions are not distinguishable between sexes. Where a species was sexually dimorphic, mean body mass was calculated. Log_{10} transformations were used on all variables, and the suggestions of Baskerville (1972) and Sprugel (1983) were followed to correct for bias when retransforming data from logarithms. All statistical analyses were carried out using S-PLUS 6.0 (Insightful Corp., Seattle, Wash.).

Results

Schoener (1968) has previously demonstrated that feeding territory size of birds has a positive, log-linear relationship to body mass. This remained true for my data set, whether migratory status was ignored ($F_{[1,49]} = 27.39$, $R^2 = 0.36$, $P = 3.45 \times 10^{-6}$; Table 2) or considered (non-migrants, $F_{[1,25]} = 9.14$, $R^2 = 0.27$, $P = 0.005$; migrants, $F_{[1,22]} = 20.94$, $R^2 = 0.49$, $P = 1.47 \times 10^{-4}$; Table 2).

A scatterplot of the relationship between the $\log_{10}$-transformed values for median natal dispersal distance and territory size demonstrated that slopes were similar for both migrants and non-migrants (Fig. 1A); thus, these two groups were initially combined for analysis of median dispersal distance.

Sutherland et al. (2000) have previously demonstrated that median natal dispersal distance of birds is positively related to body mass, and this remained true for my subsample of their data ($F_{[1,29]} = 10.26$, $R^2 = 0.26$, $P = 0.003$). There was a positive relationship between median dispersal distance and breeding territory size that was stronger than the known relationship between dispersal and body mass ($F_{[1,29]} = 20.79$, $R^2 = 0.42$, $P = 8.61 \times 10^{-5}$; Fig. 1A). The slope of this relationship was somewhat lower than 0.5 (Table 3). A multiple regression ($F_{[1,28]} = 10.79$, $R^2 = 0.44$, $P = 3.35 \times 10^{-4}$) demonstrated that although 24% of the variation in median dispersal distance was shared by both territory size and body mass, 18% of the variation in median dispersal was uniquely explained by territory size, whereas only 2% was uniquely explained by body mass. There was a positive relationship between the residuals of the median dispersal distance vs.

Table 1. Breeding territory or home-range size (ha) of some bird species.

Species	Territory size	Source(s)
Accipter cooperi	225	Schoener 1968
Accipter nisus	241	Marquiss and Newton 1981
Acrocephalus scirpaceus	0.03	Catchpole 1972
Actitis macularia	0.08	Oring et al. 1997
Aegolius funereus	2048	Hayward et al. 1993
Aphelocoma coerulescens	2.1	Schoener 1968
Aquila adalberti	1200	Ferrer and Donazar 1996
Bonasa bonasia	12	Swenson and Boag 1993; Sun et al. 2000
Bubo virginianus	212	Schoener 1968
Bucephala albeola	0.56	Gauthier 1993
Bucephala clangula	11	Eadie et al. 1995
Buteo swainsoni	246	Schoener 1968
Buteo lineatus	64	Schoener 1968
Charadrius melodius	0.40	Cairns 1982
Cygnus olor	2.2	Ciaranca et al. 1997
Dendragapus canadensis	3.3	Ellison 1971
Dendragapus obscurus	1.7	Schoener 1968
Dryocapus pileatus	263	Renken and Wiggers 1989; Bull and Holthausen 1993
Elanus leucurus	7.8	Dunk and Cooper 1994
Falco peregrinus	1256	Olsen and Olsen 1988
Falco sparverius	142	Schoener 1968
Ficedula hypoleuca	1.4	Dale and Slagsvold 1990
Hylocichla mustelina	2.7	Twomey 1945
Lagopus lagopus	2.6	Schoener 1968
Lagopus leucurus	17	Braun et al. 1993
Lanius ludovicianus	7.6	Schoener 1968
Malarus splendens	4.3	Tibbetts and Pruett-Jones 1999; Van Bael and Pruett-Jones 2000
Melospiza melodia	0.16	Schoener 1968
Motacilla alba	2.4	Houston et al. 1985
Numenius phaeopus	21	Skeel and Mallory 1996
Otus asio	58	Smith and Gilbert 1984; Sparks et al. 1994
Parabuteo unicinctus	548	Bednarz 1995
Parus caeruleus	1.6	Blondel 1985
Parus major	1.0	Both and Visser 2000
Parus palustris	2.3	Schoener 1968
Passerculus sandwichensis	0.14	Potter 1972; Welsh 1975
Passerina cyanea	0.11	Schoener 1968
Perisoreus canadensis	87	Strickland and Ouellett 1993
Pica pica	1.5	Dhindsa and Boag 1992
Picoides borealis	51	Hooper et al. 1982; Porter and Labisky 1986
Poecile atricapillus	1.5	Schoener 1968
Sayornis nigricans	0.07	Wolf 1997
Seiurus motacilla	2.0	Eaton 1958
Sitta europea	2.3	Enoksson and Nilsson 1983
Strix aluco	36	Schoener 1968
Strix nebulosa	4780	Bull et al. 1988
Strix occidentalis	806	Ganey and Balda 1989; Carey et al. 1990; Call et al. 1992; Zabel et al. 1995; Ganey et al. 1999
Toxostoma curvirostre	2.0	Fischer 1980
Turdus merula	0.73	Schoener 1968
Vireo griseus	0.13	Schoener 1968
Zonotrichia leucophrys	0.12	Patterson and Petrinovich 1978

Table 2. Parameters for cross-species regression of breeding territory size (ha) and body mass (kg) of birds.

Data[a]	Slope (SE)	Intercept (SE)	SEE
Combined	1.06 (0.20)	1.80 (0.23)	1.06
Non-migrants	0.78 (0.25)	1.85 (0.29)	1.06
Migrants	1.40 (0.30)	1.83 (0.36)	0.97

Note: Body mass was the independent variable. Only bird species that feed primarily within their breeding territory were included in analysis. Variables were $\log_{10}$-transformed. SE, standard error; SEE, standard error of the estimate.

[a] Combined data include both migrants and non-migrants.

Table 3. Parameters for cross-species regression of median natal dispersal distance (km) and breeding territory size (ha) of birds.

Data[a]	Slope (SE)	Intercept (SE)	SEE
Combined			
Raw	0.39 (0.08)	0.17 (0.13)	0.60
Residuals	0.32 (0.11)	0.00 (0.11)	0.59
Outliers removed	0.54 (0.06)	–0.08 (0.08)	0.36
Non-migrants	0.57 (0.08)	–0.16 (0.13)	0.36
Migrants	0.29 (0.14)	0.37 (0.21)	0.76

Note: Breeding territory size was the independent variable. Only bird species that feed primarily within their breeding territory were included in analysis. Variables were $\log_{10}$-transformed. SE, standard error; SEE, standard error of the estimate.

[a] Combined data include both migrants and non-migrants. Raw data do not have body mass effects removed through regression, whereas residuals do. Two outliers, *Charadrius melodius* and *Acrocephalus scirpaceus*, were removed from one analysis.

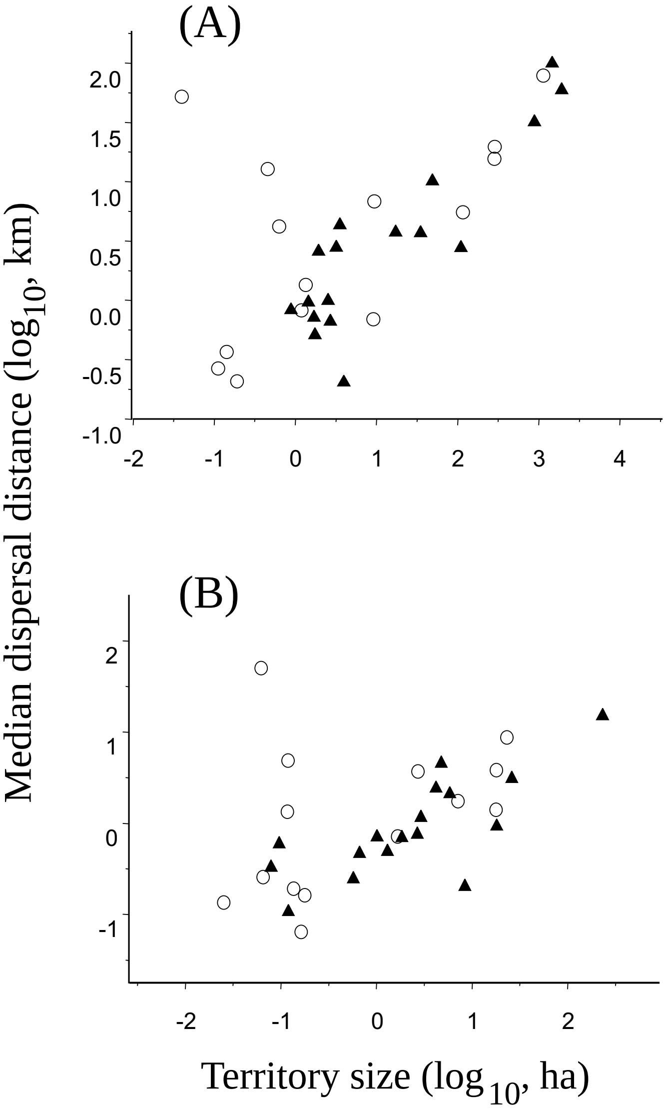
body mass regression and the residuals of the territory size vs. body mass regression ($F_{[1,29]} = 8.91$, $R^2 = 0.23$, $P = 0.005$; Table 3; Fig. 1B).

The regression between median dispersal distance and territory size contained two statistical outliers (Fig. 1). For exploratory purposes, I removed these data points (which were the Piping Plover, *Charadrius melodius*, and the Reed Warbler, *Acrocephalus scirpaceus*) and reanalyzed the data. As expected, removing these outliers strengthened the relationship ($F_{[1,27]} = 94.96$, $R^2 = 0.78$, $P = 2.47 \times 10^{-10}$) and demonstrated that the slope of the main trend was not different than 0.5 (Table 3). Retransforming these data from logarithms produced an isometric relationship between median dispersal distance and the square root of breeding territory size that can be described as

$$[2] \qquad \text{median dispersal distance} = 12\sqrt{\text{territory size}}$$

Alternatively, the same isometric relationship as described in eq. 2 was obtained when only non-migrants were analyzed ($F_{[1,15]} = 49.84$, $R^2 = 0.77$, $P = 3.87 \times 10^{-6}$; Table 3). In other words, median dispersal distance of non-migratory birds was isometrically related to the square root of territory size by a proportion of 12. When the migratory group (including the two outliers) was analyzed separately, there was a weak, positive, but allometric, relationship between median dispersal distance and territory size ($F_{[1,12]} = 4.11$, $R^2 = 0.26$, $P = 0.058$; Table 3).

Fig. 1. Relationship between median natal dispersal distance of 31 bird species and breeding territory size (A), including only bird species that feed primarily within their territory. In B, both variables are residuals after body mass (kg) has been removed through regression. Non-migrants, ▲; migrants, ○.

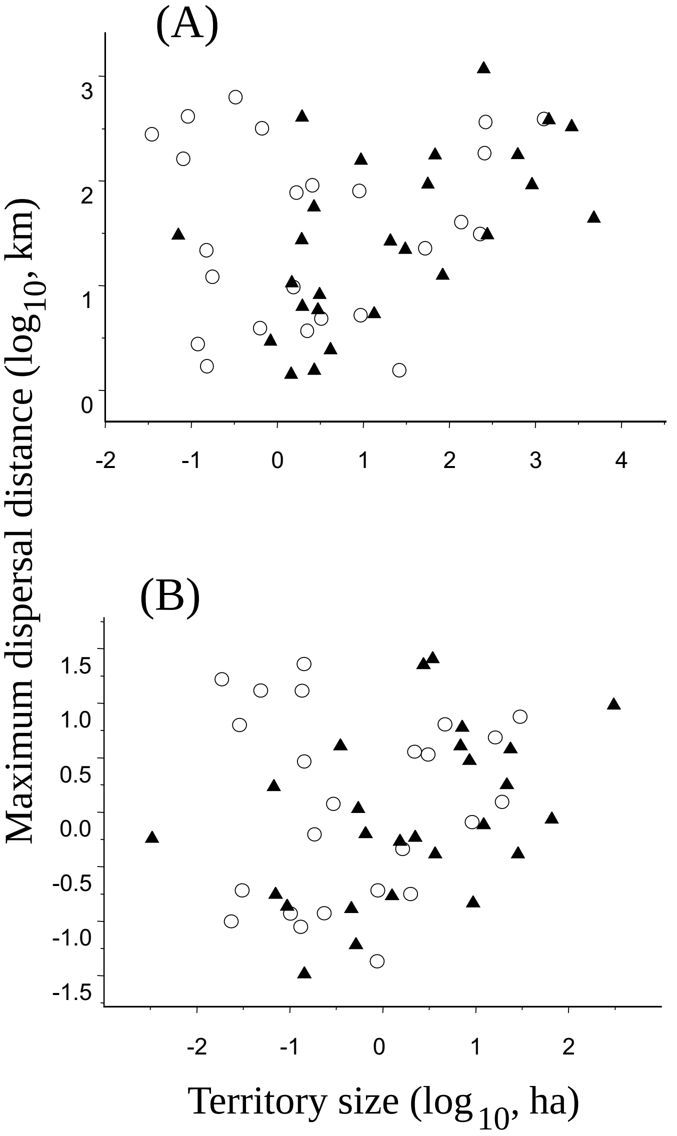


It was apparent from a scatterplot of the $\log_{10}$-transformed values for maximum natal dispersal distance and territory size that the slope of this relationship differed between migrants and non-migrants (Fig. 2A); thus, these two groups were analysed separately from the outset.

Maximum natal dispersal distance of birds is known to be positively related to body mass (Sutherland et al. 2000). This was true for the non-migrant birds in my subsample of the Sutherland et al. (2000) data set ($F_{[1,24]} = 3.56$, $R^2 = 0.13$, $P = 0.070$) but was not true for the migrants ($F_{[1,22]} = 0.11$, $R^2 = 0.01$, $P = 0.740$).

For non-migrants, there was a positive relationship between maximum dispersal distance and breeding territory size that was stronger than the known relationship between maximum dispersal and body mass ($F_{[1,24]} = 9.54$, $R^2 = 0.29$, $P = 0.005$; Fig. 2A). The slope of the relationship between dispersal distance and territory size was 0.35 (Table 4). A

Fig. 2. Relationship between maximum natal dispersal distance of 50 bird species and breeding territory size (A), including only bird species that feed primarily within their territory. In B, both variables are residuals after body mass (kg) has been removed through regression. Non-migrants, ▲; migrants, ○.



multiple regression ($F_{[2,23]}$ = 4.83, R^2 = 0.30, P = 0.018) demonstrated that 11% of the variation in maximum dispersal distance was shared by both territory size and body mass, whereas 17% of the variation in maximum dispersal was uniquely explained by territory size and only 1% was uniquely explained by body mass. There was a positive relationship between the residuals of the maximum dispersal distance vs. body mass regression and the residuals of the territory size vs. body mass regression ($F_{[1,24]}$ = 5.66, R^2 = 0.19, P = 0.025; Table 4; Fig. 2B).

For migrants, there was no detectable relationship between maximum dispersal distance and breeding territory size ($F_{[1,22]}$ = 0.35, R^2 = 0.02, P = 0.561; Table 4; Fig. 2A). A multiple regression ($F_{[2,21]}$ = 0.17, R^2 = 0.02, P = 0.843) demonstrated that <1% of the variation in maximum dispersal distance was shared by both territory size and body mass, whereas >1% of the variation in maximum dispersal was uniquely explained by territory size and <1% was uniquely explained by body mass. There was no detectable relationship between the residuals of the maximum dispersal distance vs. body mass regression and the residuals of the territory size vs. body mass regression ($F_{[1,22]}$ = 0.24, R^2 = 0.01, P = 0.625; Table 4; Fig. 2B).

Table 4. Parameters for cross-species regression of maximum natal dispersal distance (km) against breeding territory size (ha) of birds.

Data[a]	Slope (SE)	Intercept (SE)	SEE
Non-migrants			
Raw	0.35 (0.11)	1.05 (0.19)	0.69
Residuals	0.31 (0.13)	0.00 (0.13)	0.69
Migrants			
Raw	0.07 (0.13)	1.51 (0.18)	0.85
Residuals	0.09 (0.18)	0.00 (0.17)	0.85

Note: Territory size was the independent variable. Only bird species that feed primarily within their breeding territory were included in analysis. Variables were $\log_{10}$-transformed. SE, standard error; SEE, standard error of the estimate.

[a] Raw data do not have body mass effects removed through regression, whereas residuals do.

Discussion

My prediction that dispersal distance and territory size should be positively related when considered independently of body mass, was supported for median dispersal distance, regardless of migratory status, and for maximum dispersal distance of non-migrants. Median dispersal distance appeared to have a proportional relationship with territory size (i.e., the slope of this relationship was not different than 0.50). This was especially true for non-migrants but was also true for most migrant species. Because territory size (X) is a squared value, when solving for the power-law eq. 1, $X^{0.50}$ becomes $\sqrt{X}$, the square root of territory size. Thus, median dispersal distance could be related to the square root of territory size by a single constant of 12.

A positive, proportional relationship between median dispersal distance and territory size is consistent with two competing hypotheses. First, behavioural and physiological characteristics of any given species, such as diet and body shape, might have similar effects on both dispersal and within-territory movements. This would produce covariation in the extent of both kinds of movement, even after the effects of body mass are removed. I will call this the "vagility" explanation. Alternatively, dispersal distance could be a function of the distribution of vacant territories. This would produce a positive, proportional relationship only if there is a predictable distribution of territory vacancies within any given population so that, on average, the *i*th territory from any natal territory is the closest vacant one. I will call this the "vacant territory" explanation. This explanation assumes that territories within any given population are contiguous, except for exploitable vacancies, and similar in size. Or at least, variation in the spacing and size of territories within populations must be proportional across species. The vagility explanation requires no assumptions about the spacing or the size of territories to produce a positive, proportional relationship between dispersal distance and territory size. The present study cannot reject either of these hypothetical explanations. Future studies should be conducted to test whether the assumptions in the vacant territory explanation are realistic. A cursory look at the studies reviewed here suggests that they might not be (e.g., Dhindsa and Boag 1992).

Maximum dispersal distance had an allometric relationship with territory size. In other words, this relationship was non-linear when retransformed from logarithms. There are a few possible reasons why the maximum-distance data did not support my hypothesis of proportionality. First, the observed slope could be real. Large birds may disperse a shorter distance, or small birds may disperse a longer distance, than expected from isometry with territory size. Second, the observed slope could arise from measurement error. Maximum dispersal distance of birds with large territory sizes could be underestimated, relative to birds with small territories. This situation certainly is possible given that different methods of tracking birds often are used for birds at different scales. Telemetry is more prevalent for birds with large territories, but true maximum dispersers can travel out of range and be censored using this method.

I made no predictions for the effect of migratory status on the dispersal distance and territory size relationship; thus, this aspect of the study was exploratory. Dispersal distance of migrants was more weakly related to territory size than was dispersal distance of non-migrants. This occurred primarily because a number of small-bodied migrants appeared to be outliers from the central relationship between dispersal distance and territory size. The two outliers in the regression between median dispersal distance and territory size were the Reed Warbler and the Piping Plover, migrant species that occupy linear habitats. In such habitats, birds can not disperse in a random direction and it is reasonable speculation that it may take a relatively long distance for these birds to locate a suitable location to settle. Paradis et al. (1998) reached a similar conclusion about patchy habitat in their study of bird dispersal. Wolff (1999) has advocated using residuals of cross-species comparisons to uncover behavioural attributes of species, and these outliers provide such an opportunity. A similar cluster of five migrant species can be observed in the scatterplot between maximum dispersal distance and territory size (Fig. 2). Three of these species (Reed Warbler, Piping Plover, and Spotted Sandpiper (*Actitis macularia*)) occupy linear habitats.

The proportion (12) between median dispersal distance and territory size is larger than the proportion (7) between median dispersal distance and home-range size of mammals. Similarly, if one assumed an isometric relationship between maximum dispersal distance and the square root of territory size of birds, the proportion between them would be 200, which is five times greater than the appropriate proportion of 40 for mammals (Bowman et al. 2002). Clearly, the results indicate that birds disperse a relatively longer distance than do mammals.

Natal dispersal distance and breeding territory size covaried across bird species independently of body mass. Further, the results support previous research on mammals that suggested that the dispersal – home range relationship can be a useful scaling tool for ecologists. In particular, the proportional relationship between median dispersal distance and territory size suggests that some kinds of simulation and population models can be applied across species. The corollary of this idea is that modelling exercises that use median dispersal distance may be applicable to a range of species. Finally, where dispersal distances are unknown, it is straightforward to estimate median dispersal distance from territory size.

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