

RESEARCH ARTICLE

Physiological vagility and its relationship to dispersal and neutral genetic heterogeneity in vertebrates

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ABSTRACT

Vagility is the inherent power of movement by individuals. Vagility and the available duration of movement determine the dispersal distance individuals can move to interbreed, which affects the fine-scale genetic structure of vertebrate populations. Vagility and variation in population genetic structure are normally explained by geographic variation and not by the inherent power of movement by individuals. We present a new, quantitative definition for physiological vagility that incorporates aerobic capacity, body size, body temperature and the metabolic cost of transport, variables that are independent of the physical environment. Physiological vagility is the speed at which an animal can move sustainably based on these parameters. This meta-analysis tests whether this definition of physiological vagility correlates with empirical data for maximal dispersal distances and measured microsatellite genetic differentiation with distance $\{[F_{ST}/(1-F_{ST})]/\ln \text{distance}\}$ for amphibians, reptiles, birds and mammals utilizing three locomotor modes (running, flying, swimming). Maximal dispersal distance and physiological vagility increased with body mass for amphibians, reptiles and mammals utilizing terrestrial movement. The relative slopes of these relationships indicate that larger individuals require longer movement durations to achieve maximal dispersal distances. Both physiological vagility and maximal dispersal distance were independent of body mass for flying vertebrates. Genetic differentiation with distance was greatest for terrestrial locomotion, with amphibians showing the greatest mean and variance in differentiation. Flying birds, flying mammals and swimming marine mammals showed the least differentiation. Mean physiological vagility of different groups (class and locomotor mode) accounted for 98% of the mean variation in genetic differentiation with distance in each group. Genetic differentiation with distance was not related to body mass. The physiological capacity for movement (physiological vagility) quantitatively predicts genetic isolation by distance in the vertebrates examined.

KEY WORDS: Vagility, Dispersal and body mass, Genetic isolation by distance, Meta-analysis, Microsatellites

INTRODUCTION

Evolution can be defined as a change in allele frequencies within a population over time. The mechanisms responsible for changes in genetic variation over time are important for understanding biological variation and evolution. Mutations that convey a selective

advantage to an organism, whether physiological or morphological, are predicted to be perpetuated by natural selection. What is less clear is how to mechanistically explain genetic variation of selectively neutral mutations such as microsatellites. Genetic variation of neutral microsatellite loci is the most common technique used to evaluate population genetic structure (Jehle and Arntzen, 2002). One explanation to account for variation of microsatellite loci and increased meta-population structure is low gene flow. Reduced gene flow creates genetic isolation by distance (Wright, 1943) and is central to conservation and management of extant terrestrial vertebrate populations, especially with anthropogenic population displacement, climate change and habitat fragmentation (Kodandaramaiah, 2009).

Low gene flow and genetic isolation by distance are generally explained by the dispersal capacity of organisms; that is, greater genetic heterogeneity of microsatellites among populations is explained by reduced dispersal capacity. Previous studies that have examined links between genetic heterogeneity and dispersal of vertebrates generally assume that geographic factors limit dispersal and, therefore, gene flow. Although geographical barriers affect dispersal, a geographical explanation for dispersal also assumes that physiological capacity related to movement is a fixed trait within a population. However, it is clear that this is often not the case; there is considerable intraspecific variation in features that affect movement and dispersal capacity such as body mass, and physiological parameters such as metabolic capacity and the cost of transport. These variables have been largely ignored with respect to their contribution to gene flow within a population. Perhaps more importantly, when examining or comparing different patterns of genetic structure among various species, these same factors of body mass, metabolic capacity and the cost of transport should be accounted for, before assuming that geographical features primarily limit gene flow.

The central hypothesis of this analysis is that physiological vagility and its effect on the ability to disperse should strongly influence the capacity for genetic exchange and consequently the magnitude of genetic isolation by distance. Dispersal (net movement from a point of origin) strongly influences genetic isolation by distance and the demography of organisms, since it determines colonization and persistence in fragmented habitats (Lowe, 2009; Sandel et al., 2011). We introduce the concept of physiological vagility (m min^{-1}), a velocity reflecting the capacity for sustained movement, which can be quantified as the maximal sustainable metabolic rate ($\text{ml O}_2 \text{ kg}^{-1} \text{ min}^{-1}$) divided by the metabolic cost of transport ($\text{ml O}_2 \text{ kg}^{-1} \text{ m}^{-1}$). Maximal dispersal distance for individuals within a species can be empirically determined by measurements in the field. We also propose that the necessary minimum duration for dispersal (min) can be predicted as the quotient of maximal dispersal (m) and physiological vagility (m min^{-1}) (Hillman et al., 2014). Vagility has been ecologically and qualitatively defined as ‘the inherent power of movement possessed

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Received 26 March 2014; Accepted 7 July 2014

by individuals' (Allaby, 1994). In studies analysing genetic variation between populations, vagility has most often been defined by inference; that is, if genetic meta-population structure exists over short distances, then species are presumed to have low vagility (for a review, see Alex Smith and Green, 2005). In our view this is a circular argument, which is not based on any quantitative, predictive parameters for vagility.

In a previous study, we developed this quantitative metric for physiological vagility in amphibians (Hillman et al., 2014) and found that it increased with body mass and maximal dispersal distances, but was inversely related to neutral genetic heterogeneity (microsatellites). If the mechanistic physiological definition is useful in explaining interspecific genetic isolation by distance for amphibians, we postulated that it might also explain interclass variation for vertebrates in general, and for intraclass variation where the mode of locomotion differs (e.g. walking versus flying). Defining vagility from a mechanistic and physiological perspective allows quantitative tests of whether physiological capacity can explain interclass population structure of neutral microsatellite markers. Providing a quantitative definition also solves the circular problem of using a dependent variable (i.e. genetic exchange of neutral genetic markers) to define the independent variable (vagility).

Dispersal capacity is also affected by the duration of time available for movement. Vertebrate activity is environmentally influenced by photoperiod, temperature and water availability among other variables that may limit or enhance the duration that animals are able to move effectively. Interclass differences in physiological tolerance to conditions encountered during locomotion could result in differential durations of time available for movement and thus affect dispersal capacity. For example, endotherms are typically able to utilize longer daily and annual activity times than ectotherms.

Although physiology lies at the core of movement, the population genetics literature consistently fails to consider physiological phenotypes for terrestrial vertebrates. We hypothesize that species with greater dispersal capacity (i.e. greater physiological vagility and/or durations of movement) should show less neutral genetic variation with distance. The objectives of this meta-analysis were to: (1) test whether physiological vagility correlates with reported maximal dispersal capacities; and (2) test the quantitative relationship between genetic heterogeneity with distance and both dispersal capacity and physiological vagility in vertebrates. We included data derived from literature for amphibians, reptiles, mammals (terrestrial, flying and swimming) and birds. We did not include fishes in our analysis because dispersal can occur via passive water currents and via management in conjunction with the possibility of absolute movement restrictions imposed by damming.

RESULTS

The data for mass specific maximal rates of oxygen consumption ($\dot{V}_{O_{2,max}}$) used to calculate mass specific sustainable rates of oxygen consumption ($\dot{V}_{O_{2,sus}}$) for the various groups are summarized in Fig. 1. Physiological vagility (Fig. 2), calculated as $\dot{V}_{O_{2,sus}}$ divided by the minimum metabolic cost of transport (C_{min}), increased significantly ($P < 0.001$) with increasing body mass for amphibians ($r^2 = 0.197$) and terrestrial mammals ($r^2 = 0.647$). Physiological vagility increased on average with body mass for reptiles but was not significant ($P = 0.205$). Physiological vagility was independent of body mass for flying birds and flying mammals. The residual variation is principally determined by variation in $\dot{V}_{O_{2,max}}$ between the species in each group as C_{min} was calculated based upon allometric predictive equations. Because physiological vagility in

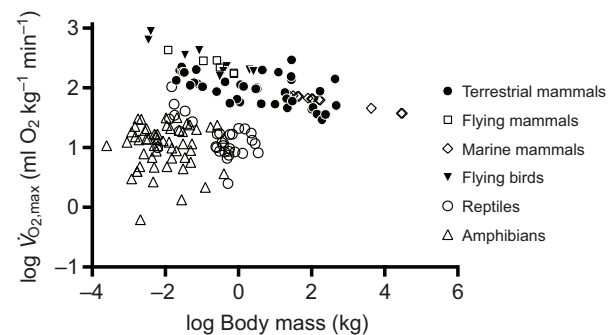


Fig. 1. Log-transformed relationship between maximal aerobic metabolic rates and typical body mass for the vertebrate species utilized for this analysis grouped by class and mode of locomotion. Data from marine mammals are extrapolated from terrestrial mammalian data.

marine mammals was based on two allometrically predicted values ($\dot{V}_{O_{2,max}}$ and C_{min}), it increased with body mass in a perfectly linear fashion.

Physiological vagility for bird flight is unique compared with terrestrial locomotion in that physiological vagility scaled independently of body mass and was much higher than in terrestrial locomotion, especially among smaller animals (Fig. 2). The data for flying mammals were limited, but appear indistinguishable from the flying bird data. Marine mammals had physiological vagilities essentially equivalent to flying animals, especially at larger body masses (Fig. 2).

The empirically determined maximal dispersal distance (D_{max}) observed for individuals within a species was analysed with respect to body mass and compared with the relationship between physiological vagility and body mass for terrestrial mammals, flying birds, reptiles and amphibians (Fig. 3). We did not include flying mammals and marine mammals in this analysis due to insufficient data. D_{max} for amphibians increased significantly with body mass ($r^2 = 0.271$, $P < 0.0001$; Fig. 3), and the allometric scaling exponent of physiological vagility (0.284) was significantly lower ($P = 0.0003$) than for D_{max} (1.05). D_{max} for reptiles also increased significantly with body mass ($r^2 = 0.804$, $P < 0.0001$; Fig. 3), and the allometric scaling exponent of physiological vagility (0.081) was significantly lower ($P < 0.0001$) than D_{max} (0.569). D_{max} for flying birds was not significantly related to body mass ($r^2 = 0.044$, $P = 0.072$; Fig. 3), similar to the independent relationship between physiological

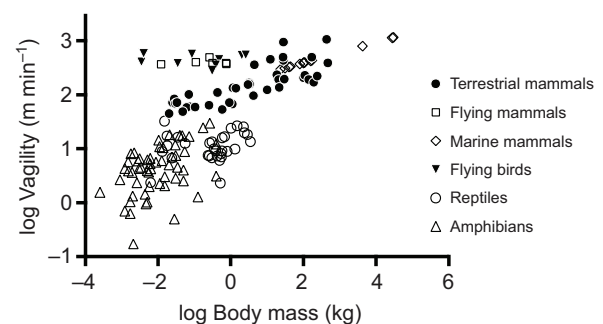


Fig. 2. Log-transformed relationship between physiological vagility and body mass for mammals (terrestrial, marine and flying), flying birds, reptiles and amphibians calculated from the metabolic data presented in Fig. 1 and C_{min} calculated for each species. Data for $\dot{V}_{O_{2,max}}$ utilized to calculate physiological vagility in marine mammals are extrapolated from terrestrial mammalian data.

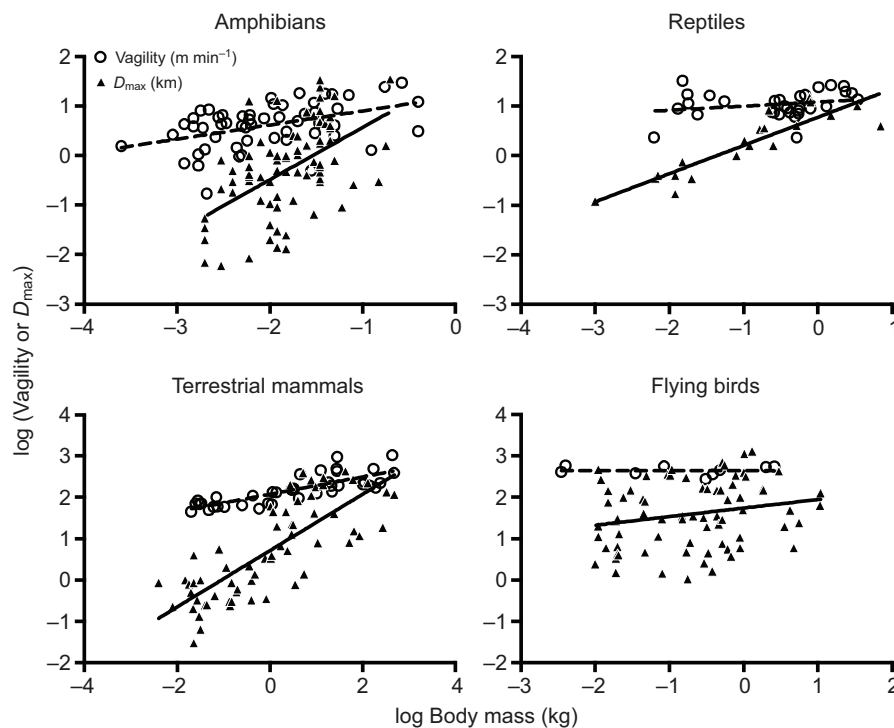


Fig. 3. Log-transformed relationship between body mass and both physiological vagility and maximal dispersal distance (D_{\max}) for amphibians, reptiles, terrestrial mammals and flying birds.

vagility and body mass, and the allometric scaling exponents of physiological vagility and D_{\max} were not significantly different ($P=0.453$). D_{\max} for terrestrial mammals increased significantly with body mass ($r^2=0.619$, $P<0.0001$; Fig. 3), and the allometric scaling exponent for physiological vagility (0.210) was significantly lower ($P<0.0001$) than D_{\max} (0.682). The means of each group for log-transformed variables (ln physiological vagility and ln D_{\max}) were positively and significantly related ($r^2=0.98$, $P=0.009$).

Genetic heterogeneity was based on neutral microsatellites and was standardized for distance $\{[F_{ST}/(1-F_{ST})]/\ln \text{distance}\}$ for all comparisons. Genetic heterogeneity was not significantly related to body mass (Fig. 4) for amphibians ($P=0.614$), reptiles ($P=0.784$), terrestrial mammals ($P=0.098$), marine mammals ($P=0.336$), flying mammals ($P=0.298$) or flying birds ($P=0.983$).

Genetic heterogeneity within the terrestrial locomotor groups was greater ($P=0.038$) and more variable ($P=0.0003$) for amphibians compared with reptiles and mammals (Fig. 5). Genetic heterogeneity for terrestrial locomotion in mammals was significantly greater ($P=0.0047$) and more variable ($P=0.0081$) than flying mammals or marine mammals (Fig. 5). However, there was no significant difference in the mean genetic heterogeneity between flying birds and flying mammals ($P=0.4072$; Fig. 5), but birds showed a significantly greater variance than bats ($P=0.0001$).

The mean of each group for genetic heterogeneity was inversely related ($r^2=0.980$, $P=0.0002$) to mean group ln physiological vagility when all classes and modes of locomotion were included (Fig. 6). The mean of each group for genetic heterogeneity was also inversely related ($r^2=0.92$, $P=0.039$) to mean group ln D_{\max} .

DISCUSSION

Our definition of physiological vagility incorporates a suite of both anatomical and physiological variables involved in locomotion including body mass, aerobic capacity, body temperature and the metabolic cost of transport. Interclass differences in these traits predict a hierarchy of values such that physiological vagility should be greatest in flying birds and flying mammals > terrestrial

mammals > reptiles > amphibians. Because C_{\min} decreases with body size, larger animals within each class will generally have a greater vagility. These hypotheses are generally supported by our analysis (Fig. 2). Typically, flying birds have greater physiological vagility than running mammals due to their higher $\dot{V}_{O_{2,\max}}$ and the lower cost of transport, while flying mammals are essentially equivalent to birds. Marine mammals that swim also have high physiological vagilities because of low metabolic cost of transport and large size. The physiological vagility advantage for terrestrial mammals, relative to terrestrial ectotherms, results from greater $\dot{V}_{O_{2,\max}}$. Differences between reptiles and amphibians were less distinct and enhanced physiological vagility in reptiles predicted due to higher operating temperatures enabling greater aerobic ability is not clearly apparent. While the increase in vagility with size was generally observed in terrestrial vertebrates, flying mammals and flying birds did not show an increase in vagility with size as $\dot{V}_{O_{2,\text{sus}}}$ decreased with size offsetting the decreased C_{\min} .

The data from our meta-analysis support a correlation between calculated physiological vagility and empirically determined maximal dispersal distance. First there is a significant correlation between physiological vagility and D_{\max} among the group means of amphibians, reptiles, flying birds and terrestrial mammals. This is a broad though significant interclass test that confirms our hypothesis that physiological vagility affects dispersal. A second test of this hypothesis involves a more specific analysis using allometry. The unifying variable between physiological vagility and D_{\max} is body mass, and both variables scale similarly with log body mass in each group. The allometric scaling relationships for physiological vagility and D_{\max} with body mass were both positive and consistently different (D_{\max} > physiological vagility) for amphibians, reptiles and terrestrial mammals. In contrast, physiological vagility and D_{\max} were independent of body mass and indistinguishable for flying birds. The general correspondence in both the class mean data analysis and the allometric analysis is remarkable when the variation in methodology for empirically determining D_{\max} in natural environments (Koenig et al., 1996) is considered. It appears that the

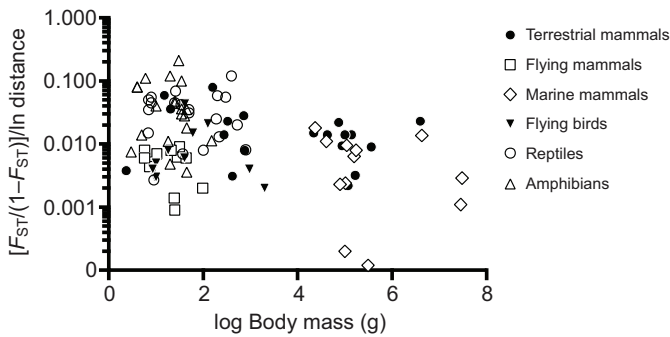


Fig. 4. Relationship between linearized genetic heterogeneity with distance and log body mass for various vertebrate classes and locomotory modes. Values are individual species mean slope values calculated from the following references: (1) amphibians (Newman and Squire, 2001; Vos et al., 2001; Lampert et al., 2003; Austin et al., 2004; Burns et al., 2004; Monsen and Blouin, 2004; Palo et al., 2004; Spear et al., 2005; Arens et al., 2006; Johansson et al., 2006; Manier and Arnold, 2006; Arens et al., 2007; Zamudio and Wiczorek, 2007; Spear and Storfer, 2008; Chan et al., 2009; Chan and Zamudio, 2009; Wang, 2009; Blouin et al., 2010; Arruda et al., 2011); (2) reptiles (Gibbs et al., 1997; Prior et al., 1997; Bushar et al., 1998; Hutchison and Templeton, 1999; Cunningham et al., 2002; Manier and Arnold, 2005; Böhme et al., 2007; Hedtke et al., 2007; Hoehn et al., 2007; Jansen et al., 2008; Johansson et al., 2008; Chan et al., 2009; Marshall et al., 2009; Prosser et al., 1999; Urquhart et al., 2009; Row et al., 2010; Klug et al., 2011; Pernetta et al., 2011); (3) flying mammals (Burland et al., 1999; Castella et al., 2000; Castella et al., 2001; Campbell et al., 2006; Racey et al., 2007; Rossiter et al., 2007; Ngamprasertwong et al., 2008; Salgueiro et al., 2008; Chen et al., 2010; Floyd et al., 2010; Chinnasamy et al., 2011); (4) terrestrial mammals (Forbes and Hogg, 1999; Gerlach and Musolf, 2000; Girman et al., 2001; Comstock et al., 2002; Yu and Peng, 2002; Møller et al., 2004; Cronin et al., 2005; Trizio et al., 2005; Lampila et al., 2009; McDevitt et al., 2009; Schmidt et al., 2009; Floyd et al., 2011; Frantz et al., 2012; Thimmayya and Buskirk, 2012); (5) marine mammals (Valsecchi et al., 1997; Escorza-Treviño and Dizon, 2000; Hoelzel et al., 2002; Larson et al., 2002; Krützen et al., 2004; Trujillo et al., 2004; Adams and Rosel, 2006; Quérouil et al., 2007; Graves et al., 2008; González-Suárez et al., 2009; Herreman et al., 2009; Dickerson et al., 2010; Mendez et al., 2010); and (6) birds (Gibbs et al., 2000; Lee et al., 2001; Williams et al., 2002; Tiedemann et al., 2004; Burg et al., 2005; Davis et al., 2006; Johnsen et al., 2006; Funk et al., 2007; Koopman et al., 2007; Nittinger et al., 2007; Barr et al., 2008; Hull et al., 2008; Lindsay et al., 2008; Pavlacky et al., 2009; Bicknell et al., 2012).

general characteristics of each class that affect physiological vagility have a measurable correlation with the average dispersal within each class despite enormous intraclass variation. Within each class, the wide variation in physiological vagility correlates overall with dispersal, despite the tremendous variation between species relative to their life history and the variation in methodology to measure aerobic capacity and D_{\max} .

While physiological vagility would affect dispersal, the time that an organism moves would clearly also affect dispersal distances. For example, the duration of time available for movement differs between groups, such as endotherms that have greater daily and seasonal potential for dispersal compared with ectotherms, and reptiles whose greater tolerance of dry air compared with amphibians allows longer activity periods. The greater slopes of D_{\max} compared with vagility with body mass for terrestrial locomotion would indicate that larger animals require longer movement durations to achieve D_{\max} . For flying vertebrates, the similar allometric relationship for D_{\max} and physiological vagility with body mass indicates that physiological vagility is the primary determinant of D_{\max} and that size would not greatly affect the durations of movement necessary to achieve D_{\max} .

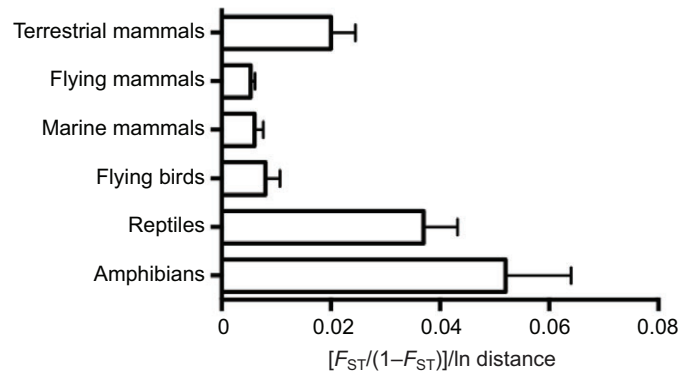


Fig. 5. Linearized genetic heterogeneity with distance for various classes and modes of locomotion. Values are the means \pm s.e.m. of each group calculated from the references in Fig. 4.

The duration of time (h) required to achieve D_{\max} at an aerobically sustainable speed is equal to D_{\max} (m) divided by vagility (m/h). When plotted relative to body mass (Fig. 7), there is clear variability between the groups, but in all groups there is an increase in the time necessary to achieve D_{\max} with increases in body mass. However, the greatest time necessary to achieve D_{\max} is less than 10 h in all groups except for the largest members of each group. Again, birds are unique in that species of all sizes could reach D_{\max} in less than 10 h. This indicates that maximal dispersal distances can be reached in a relatively short amount of time and that this type of movement represents a very small fraction of an annual activity budget. It may also indicate that $\dot{V}_{O_{2,sus}}$ is a smaller fraction than 60% of $\dot{V}_{O_{2,max}}$ that we used to determine physiological vagility necessitating longer durations of activity for dispersal.

Genetic heterogeneity with distance was inversely related to both empirical data for D_{\max} and physiological vagility as predicted from our isolation by distance hypotheses (Fig. 6). Recognize, however, that these represent a mean group physiological vagility and D_{\max} of the species within each group where data were available. The genetic heterogeneity data were taken from studies where F_{ST} and distance between the populations sampled was available. Given these broad parameters and differences in both axes the relationship appears robust. Our physiological vagility metric does not exclude landscape (Adriaensen et al., 2003; Storfer et al., 2007; Jaquière et al., 2011) and ecological variables (Hokit et al., 2010) as also playing a role in explaining variation in genetic exchange. Distance,

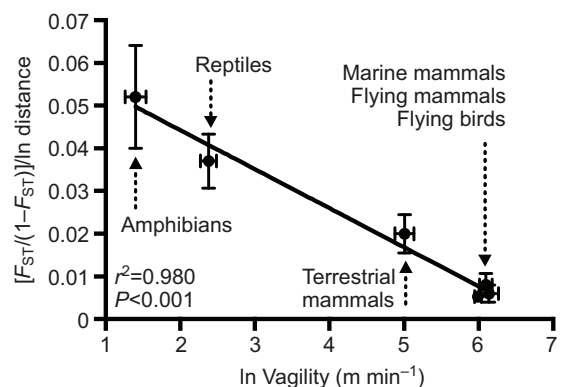


Fig. 6. Relationship between genetic heterogeneity with distance and ln mean physiological vagility for each category (class and mode of locomotion) delineated in Fig. 5. Values represent group means \pm s.e.m.

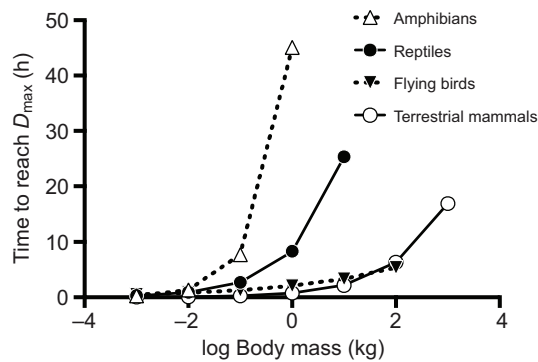


Fig. 7. A representation of the time it would take to achieve maximal dispersal distances (D_{\max}) if operating at a sustainable velocity, our measure of vagility, for mammals (terrestrial), flying birds, reptiles and amphibians of different body mass.

elevation change, roads, clear cuts, water and other geographical barriers can all clearly play a role in limiting movement and genetic exchange. Mechanistically, landscape variables can indirectly reflect mortality or induce physiological stresses limiting movement. A low mean and variance of the genetic heterogeneity metric with distance suggests that landscape variables are relatively insignificant in comparison with the inherent physiological capacities within a class. In this regard terrestrial locomotion compared with flight and swimming shows greater mean and variance of genetic heterogeneity, suggesting that geography is less important in flight and swimming, and this matches logical expectations. The significantly greater variance of genetic heterogeneity in amphibians compared with mammalian terrestrial locomotion might suggest that physical environmental variables are more significant for amphibians than mammals. This makes intuitive sense because amphibians in general are much smaller than mammals and similar geographical barriers will have a greater impact on amphibian movement. It is also important to recognize that body temperature during the breeding season will also affect $\dot{V}_{O_{2,sus}}$ and the resultant vagility for amphibians (Hillman et al., 2014).

There are several ways in which this meta-analysis is potentially flawed. The first is the absence of simultaneous data for each species for the variables included in the analysis. Species-specific measurements of C_{\min} would be advantageous for incorporation of a standard allometrically derived C_{\min} used for each mode of locomotion. Similarly, our definition of $\dot{V}_{O_{2,sus}}$ as 60% of $\dot{V}_{O_{2,max}}$ is probably an overestimate of normal locomotor behavior in many species and utilization of speeds even within an 'aerobic' range below the anaerobic threshold would cause fatigue if utilized for extended periods. The term sustained metabolic scope has also been used to describe energy budgets that were integrative of both rest and activity periods, and expressed as multiples of $\dot{V}_{O_{2,rest}}$ (Peterson et al., 1990). Their conclusion was that sustained metabolic rate was somewhere between two and seven times the resting value, which would approximately translate into 20–70% of $\dot{V}_{O_{2,max}}$ and would be inclusive of our 60% value. However, the fraction of $\dot{V}_{O_{2,max}}$ chosen could change the conclusions we reach in two ways. First, if $\dot{V}_{O_{2,sus}}$ was a smaller fraction than 60% of $\dot{V}_{O_{2,max}}$ the time necessary to achieve D_{\max} would increase. Second, if the fraction varied between the various classes and modes of locomotion the conclusions might be very different. There are no data to suggest that this fraction varies significantly between classes, but variation probably exists and more data would further inform our conclusions. C_{\min} values for each species involved in the analysis would probably not influence

the conclusions significantly as the cost of transport data for different locomotor modes are quite robust.

The degree of interspecific variance of genetic heterogeneity described by this single physiological metric of vagility is greater than the intraspecific variance explained by analyses of multiple environmental and landscape characteristics that fail to incorporate vagility as a metric. The most important point resulting from our meta-analyses is that interclass differences in physiological vagility resulting from physiological and anatomical phenotypes play a significant role in determining genetic exchange among vertebrates (Fig. 6). A logical extension of this clear relationship suggests that variation in intraclass vagility would also play an important explanatory role for variation in genetic exchange between species for other vertebrates, as observed in amphibians (Hillman et al., 2014). The selection pressures that led to different modes of locomotion, body size and aerobic capacity are distinct from the resultant population genetic consequences. Inherent physiological differences should be considered in addition to both ecological and landscape environmental variables previously used to describe observed neutral genetic variation of vertebrate populations.

The meta-analysis supports 'neutrality' for microsatellite markers. Vagility alone, reflecting dispersal capacity, explaining 98% of the variation in genetic heterogeneity between groups of amphibians, reptiles, mammals and birds argues against selection operating on microsatellite markers. We question the usefulness of using neutral markers in conservation genetics, especially if the F_{ST} data simply reflect variation in physiological vagility influencing dispersal distances. We suggest that quantifying heterogeneity between populations using genetic markers that reflect selective differences would represent a more informative method for effective conservation of important genetic information, rather than maintenance of genetic variation in neutral microsatellite markers.

MATERIALS AND METHODS

This meta-analysis required four types of literature data to be summarized: the maximal rate of mass specific oxygen consumption ($\dot{V}_{O_{2,max}}$), the mass specific metabolic cost of transport (C_{\min}), maximal dispersal distances (D_{\max}) and the relationship of neutral microsatellite genetic heterogeneity with distance.

Physiological vagility

Physiological vagility is the maximal sustainable locomotor velocity (distance over time) that can be achieved by an organism. The variables that contribute to this velocity include two physiological metrics: (1) the mass-specific maximal sustainable metabolic rate of the species ($\dot{V}_{O_{2,sus}}$), and (2) the minimum metabolic cost of transport (C_{\min}).

There is extensive literature on resting and maximal rates of \dot{V}_{O_2} for vertebrates. The uncertainty is that prolonged, sustainable locomotion is a fraction of $\dot{V}_{O_{2,max}}$, but is less commonly measured, and in reality no level of activity is truly sustainable. $\dot{V}_{O_{2,sus}}$ in theory is a metabolic rate that can be maintained aerobically without the accumulation of anaerobic metabolic products that contribute to fatigue and negatively impact endurance. At greater intensities, where O_2 delivery and concomitant mitochondrial ATP production does not match the total rate of ATP consumption, anaerobic products accumulate and locomotion is no longer sustainable, even if the metabolic rate remains below $\dot{V}_{O_{2,max}}$. Typically, $\dot{V}_{O_{2,sus}}$ is 50–80% of $\dot{V}_{O_{2,max}}$ in the four tetrapod vertebrate classes (Davis et al., 1979; Seeherman et al., 1983; Gleeson and Brackenbury, 1984; Taigen and Beuchat, 1984). We have chosen an admittedly arbitrary but constant and intermediate value of 60% of $\dot{V}_{O_{2,max}}$ as $\dot{V}_{O_{2,sus}}$ in order to provide a metric that is comparable between species and proportional to their differing aerobic abilities, but conservative relative to a speed that most animals can sustain.

Physiological vagility ($m \min^{-1}$) is then defined as:

$$\text{Physiological vagility} = \dot{V}_{O_{2,sus}}/C_{\min}, \quad (1)$$

where $\dot{V}_{O_{2,sus}}$ is in ml O₂ kg⁻¹ min⁻¹ at standard temperature and pressure (dry) and C_{min} is in ml O₂ kg⁻¹ m⁻¹.

The available data for maximal aerobic metabolic rate ($\dot{V}_{O_{2,max}}$) utilized to calculate $\dot{V}_{O_{2,sus}}$ for this summary were obtained from the following sources: amphibians (Gatten et al., 1992); reptiles (Bennett, 1972; Bennett, 1982); birds (Tucker, 1968; Tucker, 1972; Bernstein et al., 1973; Hudson and Bernstein, 1983; Suarez et al., 1991; Chappell et al., 1996; Bundle et al., 1999; Ward et al., 2002; Ellerby et al., 2003) and mammals (Thomas, 1975; Lechner, 1978; Thomas et al., 1984; Carpenter, 1985; Carpenter, 1986; Lindstedt et al., 1991; Widmer et al., 1997; Winter, 1998; Young et al., 2002; Weibel et al., 2004).

The $\dot{V}_{O_{2,max}}$ for amphibians and reptiles is temperature sensitive and normally increases 2- to 3.3-fold for every 10°C increase in temperature (i.e. Q_{10}). We used values for $\dot{V}_{O_{2,max}}$ at 20–25°C for amphibians and 30–35°C for reptiles where these species are optimized to operate at a high sustainable metabolic rate. Endothermic $\dot{V}_{O_{2,max}}$ is reported for normal body temperature though at $\dot{V}_{O_{2,max}}$ their body temperatures will normally be elevated from the high rate of heat production. Data for $\dot{V}_{O_{2,max}}$ of marine mammals are limited, and so were extrapolated based on body mass from the $\dot{V}_{O_{2,max}}$ for the terrestrial mammal data in this meta-analysis using the following equation: $\dot{V}_{O_{2,max}}=2.022M_b^{0.900}$, where M_b is body mass (kg).

Typical body masses of ectotherms were derived from a variety of field guides and literature, and for endotherms were derived from Dunning (Dunning, 1992) and Smith et al. (Smith et al., 2003). Typical body masses of each species were utilized to calculate the species specific C_{min} based on their mode of locomotion.

C_{min} (ml O₂ kg⁻¹ m⁻¹) was estimated for each species using the summary formulae of Gatten et al. (Gatten et al., 1992) for terrestrial locomotion ($C_{min}=0.53M_b^{-0.31}$), Tucker (Tucker, 1970) for flight ($C_{min}=0.26M_b^{-0.23}$) and Williams (Williams, 1999) for swimming marine mammals ($C_{min}=0.39M_b^{-0.29}$). The C_{min} (energy per mass per distance) tends to occur at a speed that correlates with $\dot{V}_{O_{2,sus}}$ such that the transport costs we apply here are most applicable for long and sustained movement.

Maximal dispersal distances

There are multiple empirical methods for determining D_{max} including mark-recapture, trapping, radio-tracking and genetic analyses. The size of monitored areas varies between studies as well as the duration of monitoring (months, seasons, years) so there are inherent biases in literature summaries, the precision is low, and large variation is expected (Koenig et al., 1996).

We collected literature values for maximal reported dispersal distances and the associated typical body mass for each species from multiple sources. The D_{max} for amphibians are from a summary (166 articles, 90 species) compiled by Alex Smith and Green (Alex Smith and Green, 2005) and we estimated typical body masses of each species from field guides and the literature. The D_{max} and typical body mass values for reptiles were taken from a variety of studies (Noble and Clausen, 1936; Hirth et al., 1969; Brown and Parker, 1976; Wiewandt, 1977; Werner, 1983; Larsen, 1987; Brown and Brooks, 1994; Madsen and Shine, 1996; Plummer, 1997; Pough et al., 1998; Hokit et al., 1999; Blouin-Demers and Weatherhead, 2002; Middendorf et al., 2005; Marshall et al., 2006; Keogh et al., 2007; Dubey et al., 2008; Rutherford and Gregory, 2003; Templeton et al., 2011; Warner and Shine, 2008; Welsh et al., 2010). The D_{max} and typical body mass values for birds and mammals were taken from Sutherland et al. (Sutherland et al., 2000). In these studies, estimations of D_{max} were made on individuals naturally dispersing within their own home ranges, and did not include migratory movements. If multiple determinations were reported for the same species, the highest D_{max} for that species was utilized.

Correlation between physiological vagility and D_{max}

Since the data we utilized for estimations of D_{max} have little species overlap with the data utilized for estimations of physiological vagility, we attempted to standardize both D_{max} and physiological vagility by analysing their relationship to body mass simultaneously (Fig. 3). Body mass is allometrically related to D_{max} and to both variables used to calculate physiological vagility ($\dot{V}_{O_{2,sus}}$ and C_{min}), so the analyses utilized log transformations of all three variables. It is important to recognize that the variation in method and scope of measurements for D_{max} will introduce

greater intraclass variation than our estimates of vagility, but the overall relationships to body mass can be informative.

Duration of movement

The duration of movement (min) necessary for dispersal can be defined as:

$$\text{Duration of movement} = D_{max}/\text{physiological vagility}, \quad (2)$$

where D_{max} is in m and physiological vagility is in m min⁻¹.

Similar allometric relationships with D_{max} and physiological vagility with body mass would predict a consistent duration of movement necessary to achieve D_{max} .

Genetic heterogeneity with distance

Analysis of presumably neutral microsatellite markers is the most common current technique used to evaluate population genetic structure at a geographical scale (Jehle and Arntzen, 2002). Genetic differentiation of populations is generally estimated by F_{ST} (the proportion of the variance in allele frequencies present among populations). Variation in microsatellite loci with geographic distance has been used to infer gene flow (isolation by distance) and establishing meta-population structure (Jehle and Arntzen, 2002). The majority of these studies suggest that genetic heterogeneity increases with distance; however, it is difficult to interpret an absolute F_{ST} value directly as different studies report their results over different mean geographic distances. Instead, we have used the slope of the relationship between F_{ST} [$F_{ST}/(1-F_{ST})$] and ln distance (km). The common procedure to determine whether isolation by distance is present is the Mantel test, which determines whether there is a positive correlation between F_{ST} and ln distance (Rousset, 1997; Rousset and Raymond, 1997). We are essentially applying a regression analysis rather than a correlation to normalize all the studies to ln distance. The values we report are the mean of all population comparisons that are significantly different from one another in a particular study.

Statistics

Least-squares linear regression techniques were used to determine relationships. Comparisons were made via ANOVA. All statistical comparison were performed with Prism version 6.0 (GraphPad Software, La Jolla, CA, USA).

Acknowledgements

Dr Phil Withers, Dr Art Woods, Dr Michael Murphy and two anonymous reviewers provided valuable feedback on the manuscript.

Competing interests

The authors declare no competing financial interests.

Author contributions

All authors participated equally in data summary, the development of ideas and writing the manuscript.

Funding

This work was supported by the National Science Foundation (IOS-0843082).

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