Comparative Biochemistry and Physiology, Part A 223 (2018) 42–51

Contents lists available at ScienceDirect

Comparative Biochemistry and Physiology, Part A

journal homepage: www.elsevier.com/locate/cbpa

# Physiological vagility affects population genetic structure and dispersal and enables migratory capacity in vertebrates

Thomas V. Hancock[a,*,1], Michael S. Hedrick[b,1]

[a] Department of Biology, Portland State University, Portland, OR 97201, USA
[b] Department of Biological Sciences, California State University, East Bay, Hayward, CA 94542, USA

ARTICLE INFO

*Keywords:*
Physiological vagility
Population structure
Genetic isolation by distance
Dispersal
Migration
Vertebrates

ABSTRACT

Vagility is defined as the relative capacity for movement. We developed previously a quantitative metric in vertebrates for physiological vagility (PV), the speed at which an animal can move sustainably, incorporating aerobic capacity, body size, body temperature, and transport costs, allowing quantitative tests of whether PV can explain variation in interclass population genetic structure and behaviors involved in dispersal. We found that PV increased with body mass, correlated with maximal dispersal distances, and was inversely related to genetic structure in multiple vertebrate groups. Here we review these relationships and expand our analysis to include additional groups; we also suggest that PV may be utilized to partially explain variation in migratory capacity between groups. We show a positive correlation between PV and maximum migration distance ($M_{MAX}$) in most groups that reflects many of the relationships observed between PV and dispersal. Flying birds, marine mammals, and large terrestrial mammals display the greatest $M_{MAX}$ and each of these groups has the highest PV among vertebrate groups, while reptiles and small terrestrial mammals had the lowest PV and $M_{MAX}$. By contrast, marine turtles have exceptional $M_{MAX}$ but do not possess high PV. We suggest that PV is an important mechanism enabling both dispersal and migratory capacity, and affects genetic structure, but that other life history characteristics also need to be considered.

## 1. Introduction

### 1.1. Physiological vagility (PV), dispersal and genetic structure

The genetic structure of populations, reflecting neutral genetic heterogeneity, describes the genetic relatedness of various populations that are connected by dispersal and are part of a larger metapopulation that extends across the landscape (Marsh and Trenham, 2001). Many studies define population structure and connectivity based on genetic polymorphism data, such as single-nucleotide polymorphisms (SNP) or microsatellites, and utilize measures such as the fixation index ($F_{ST}$), among others. The origin of this genetic diversity is the basis of potential speciation. Within historical biogeography, speciation is classically thought of as being either due to vicariant (isolating) events and fragmentation of populations or due to dispersal across pre-existing barriers and eventual isolation (Zink et al., 2000). Low gene flow and genetic isolation by distance are generally explained by reduced dispersal capacity across such barriers.

Most previous studies that have examined links between genetic structure and dispersal of vertebrates generally assume that geographic factors limit dispersal and, therefore, gene flow. However, most of these studies typically pay little attention to the vagility of organisms (Kodandaramaiah, 2009), which has been ecologically and qualitatively defined as "the inherent power of movement possessed by individuals" (Allaby, 1994). Vagility varies within and between species and is determined by factors that affect the cost of transport such as body mass and locomotor mode, as well as factors such as body temperature and metabolic capacity. In studies analyzing 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 (see Kodandaramaiah, 2009). In our view, this is a circular argument, which is not based on any quantitative, predictive parameters for vagility. Instead, when examining or comparing different patterns of genetic structure among various species, the vagility inherent to an organism should be accounted for before assuming that geographic features primarily limit gene flow (Seebacher and Franklin, 2012).

Our previous work defined these combined factors that affect vagility within various vertebrate species as physiological vagility (PV; $m\,min^{-1}$) which is a velocity reflecting the capacity for sustained

* Corresponding author at: 1825 SW Broadway, Portland, OR 97201, USA.
*E-mail address:* thancock@pdx.edu (T.V. Hancock).
[1] These authors contributed equally to this study.

https://doi.org/10.1016/j.cbpa.2018.05.015
Received 15 December 2017; Received in revised form 10 May 2018; Accepted 11 May 2018
Available online 18 May 2018

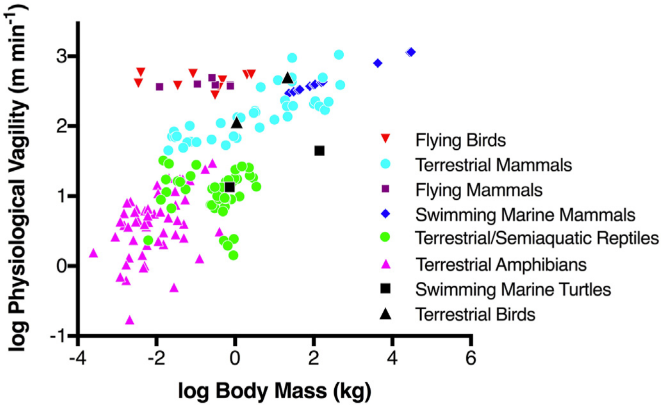


**Fig. 1.** Physiological vagility vs. body mass. Log transformed relationship between physiological vagility (PV; $m\,min^{-1}$) and body mass (kg) in multiple groups of vertebrates separated by class and mode of locomotion. As previously described (Hillman et al., 2014a), with further data from additional terrestrial reptiles, marine turtles and terrestrial bird data points as referenced in methods. Modified from (Hillman et al., 2014a).

movement (Hillman et al., 2014a,b). PV was quantified as the mass-specific maximal sustainable aerobic metabolic rate ($VO_{2SUS}$) divided by the mass-specific minimum metabolic cost of transport ($C_{MIN}$) for each species.

$$PV\,(m\,min^{-1}) = VO_{2SUS}\,(ml\ O_2 kg^{-1} min^{-1})/C_{MIN}\,(ml\ O_2 kg^{-1} m^{-1})$$

$VO_{2SUS}$ for an animal was defined as 60% of the maximal aerobic metabolic rate, a general measure of the point at which anaerobic capacity begins to be utilized and thus velocities above this are considered to be unsustainable. For $C_{MIN}$, it is well-established that for a given body mass $C_{MIN}$ is lowest for swimming animals, followed by flying animals, while terrestrial locomotors (runners/walkers) have the greatest $C_{MIN}$. Thus, for a given body mass and $VO_{2SUS}$, PV is highest for swimmers, followed by flyers, and is lowest for runners/walkers.

PV was regressed against body mass in the various vertebrate groups (Fig. 1). PV increases with body mass in terrestrial mammals, amphibians, and swimming marine mammals. However, no relationship was seen with body mass in flying birds and flying mammals, resulting in a constant PV in all flyers that is also high among vertebrates due to the low $C_{MIN}$ and the high rates of aerobic metabolism among these endotherms. Among terrestrial mammals and amphibians as well as marine mammals, PV increases with body mass primarily due to the decrease in $C_{MIN}$ associated with increased body mass. The largest swimming and terrestrial endotherms thus achieve high PV comparable to flyers. Ectothermic amphibians and reptiles have lower PV than endotherms at any given body mass due to lower aerobic capacity, and PV is also generally lower in these groups overall due to decreased body size. The terrestrial and semiaquatic reptiles analyzed do not exhibit a significant relationship between PV and body mass indicating that other variations among lizards, turtles, snakes and crocodilians have a greater impact on PV than does body mass.

Among amphibians, reptiles, flying birds and terrestrial mammals it was demonstrated that the relationships between maximal dispersal distances ($D_{MAX}$) and body mass were similar to the relationships between PV and body mass (Hillman et al., 2014a). This indicates that the physiological characteristics that determine greater PV in a species tended to also drive a higher observed dispersal capacity in a species. In most cases, the measures of $D_{MAX}$ that we adopted were based on measures of natal dispersal which is often described as a fundamental element of demography, population dispersal, colonization and gene flow (Sutherland et al., 2000). When comparing vertebrate groups that differ substantially in their PV, a significant positive correlation to the average $D_{MAX}$ of each group is observed (Fig. 2) indicating that PV drives dispersal capacity overall in each group based on the broad

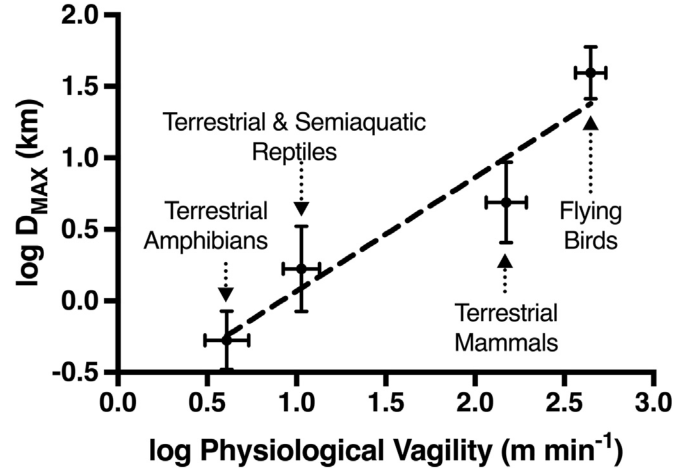


**Fig. 2.** Dispersal capacity vs. physiological vagility. The significant log transformed relationship ($p = 0.044$; $R^2 = 0.914$.) between group means of maximal dispersal capacity ($D_{MAX}$; km) as a function of group means of physiological vagility (PV; $m\,min^{-1}$) for amphibians (N = 55,77), terrestrial and semiaquatic reptiles (N = 42,20), terrestrial mammals (N = 40,63), and flying birds (N = 9,75). Sample sizes given for PV and $D_{MAX}$, respectively. Error bars represent the 95% confidence interval.

differences between groups in both aerobic capacity and the mode of locomotion that is utilized.

We hypothesized that because PV affects the ability to disperse, it should consequently explain much of the variation in genetic structure between various vertebrate species. Genetic structure, reflecting neutral genetic heterogeneity, as defined previously (Hillman et al., 2014a) was quantified using measured microsatellite genetic differentiation with distance ($(F_{ST}/1 - F_{ST})$ / ln km) in order to compare relative genetic differentiation between species and groups. Because microsatellites are neutral genetic markers, variation reflects genetic exchange and not adaptation. Mean genetic structure was compared among the same vertebrate groups and regressed against the mean PV of each group (Fig. 3a) demonstrating a significant negative relationship where the mean PV of different groups (class and locomotor mode) accounted for 98% of the variation in mean genetic structure among groups. Genetic structure was greatest for amphibians, correlating with the lowest overall PV. Flying birds, flying mammals, and swimming marine mammals with the highest PV demonstrated the least genetic structure and the mean values of both measures were surprisingly similar in these three groups. Terrestrial mammals and reptiles showed intermediate PV that correlated with the genetic structure of each group. These data demonstrate that PV explains a great deal of interclass variation in genetic structure over a wide range of vertebrate classes with diverse locomotory modes (Hillman et al., 2014a,b).

Intraspecific variation in PV should also be considered. For example, among European badgers, dispersing males had a larger average body size, which would correspond to a larger PV, in comparison to those males that did not disperse (Woodroffe et al., 1995). A dichotomy might especially exist where there is large intraspecific variation in body size, such as between the sexes in sexually dimorphic species. While females tend to be larger than males in most sexually reproducing animals (Andersson, 1994), mammals as a class tend to have larger adult males than females in nearly every group examined (Lindenfors et al., 2007), which would consequently increase PV in males in comparison with females. In mammals, males also tend to disperse more widely than females overall (Greenwood, 1980) and the higher PV in males would make this possible. Among many species, this is demonstrated in mountain gorillas (*Gorilla beringei beringei*) where male dispersal is greater than female dispersal, and this consequently decreases genetic structure among males in comparison to females (Roy et al., 2014).