

A mobility index for Canadian butterfly species based on naturalists' knowledge

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Abstract Mobility is a key component of species' biology. Research on mobility is inherently difficult, however, resulting in studies of narrow taxonomic, spatial, and temporal scope with results that are difficult to compare between studies. We had three goals for our research: (1) construct a data set of mobility estimates for the butterfly species of Canada based on naturalists' knowledge; (2) develop methods to evaluate aspects of accuracy and precision for knowledge-based ecological research such as ours; and (3) using our data set, test mobility-related hypotheses of species-level relationships. We distributed a questionnaire to amateur and professional lepidopterists in Canada and northern USA, asking them to estimate the mobility of Canadian butterfly species based on their field experience. Based on responses from 51 lepidopterists with approximately 800 years of combined field experience, we received mobility estimates for almost all (291 out of 307) of Canada's butterfly taxa. Mobility estimates were consistent among respondents and were not affected by respondent expertise. Mobility carries a strong phylogenetic signal and is positively related to wingspan (albeit weakly), range size, and host plant breadth, and negatively related to conservation risk. Reliance upon naturalists' experience was essential to the feasibility of our project, and provides a promising method for many types of ecological research.

Keywords Dispersal · Expert opinion · Lepidoptera · Life-history strategy · Local ecological knowledge · Movement ecology · Naturalists · Phylogenetic signal · Questionnaire · Range size

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Abbreviations

ACDC	Accelerating-Decelerating
AIC	Akaike's Information Criterion
FDR	False discovery rate
GLS	Generalized least squares
IC	Independent contrast
LEK	Local ecological knowledge
OLS	Ordinary least squares
OU	Ornstein-Uhlenbeck
PCA	Principal Components Analysis

Introduction

Mobility is a core component of species' ecology and evolution (Ronce 2007), and is important for conservation because it can affect species' responses to habitat fragmentation (Hendrickx et al. 2009) and climate change (Pöyry et al. 2009). The trouble with mobility, from a researcher's perspective, is that it is difficult to study. A recent literature review found that although the number of publications on movement ecology is increasing rapidly, these studies tend to focus on narrow aspects of movement and on only one or a few species (Holyoak et al. 2008). Integration of the many disciplines related to mobility is inhibited in part by terminology differences between researchers of various taxonomic groups (Holyoak et al. 2008). We use movement and mobility interchangeably throughout this paper, referring to local-scale movement within or between habitat patches, and follow Bowler and Benton's broad definition of dispersal as movement between habitat patches (2005). In addition to the varied terminology, the very nature of movement makes it difficult to quantify in ways that are not species- or location-specific. This difficulty has resulted in the use of a variety of methods to study mobility, each with advantages and limitations (Table 1), and some methods producing results more similar to each other than others (Stevens et al. 2010b). While large data sets for ecological and life-history traits have accumulated for many model taxa including butterflies (Dennis et al. 2008), movement data sets have generally remained small-scale and difficult to compare across studies, locations, and taxa. Unless we consider unconventional research methods to obtain large amounts of movement data quickly and cost-effectively, this trend is unlikely to change and researchers investigating trends across large numbers of taxa may ignore movement or use potentially inappropriate proxies for it in their research.

Butterflies provide a good taxonomic group to investigate mobility. It has been argued that dispersal is better documented for butterflies than for any other group of animals, which, combined with the importance of dispersal and mobility for butterflies, makes them a model system for mobility research (Stevens et al. 2010b). Butterfly mobility results can be understood in a wide biological context because butterfly ecology has been well-studied (Dennis et al. 2008) and phylogenetic relationships are well resolved (Wahlberg et al. 2005). Further, butterflies are used as model taxa in conservation research on responses to habitat change (Thomas 2005; Öckinger et al. 2010) and climate change (Parmesan 2003), allowing research on the influence of mobility on species' responses to modern threats.

Table 1 Comparison of methods available to investigate terrestrial insect movement

Method	Advantages	Limitations	Example
<i>Mark-release-recapture</i> . Individuals are marked and released, with the distance between release and subsequent recapture locations used as dispersal distance	Biologically intuitive measure of dispersal	Spatial scale of study affects results (Schneider 2003) Large number of marked individuals required (Franzén and Nilsson 2007), limiting research to abundant species Generalization beyond the location of the study requires consideration of landscape factors (Dover and Settele 2009)	Franzén and Nilsson (2007)
<i>Genetic differentiation</i> . Genetic distance between populations used to infer gene flow and dispersal	Allows standardized methods and comparisons across taxa Allows investigation at large spatial and temporal scales	Incorporates not only dispersal, but also successful colonization, sexual selection, and reproduction (Keyghobadi et al. 2003) Population-scale measure that ignores individual variation Results can depend on which locus is used (e.g., Zakharov and Hellmann 2008)	Keyghobadi et al. (2003)
<i>Harmonic radar</i> . Small antennae attached to individual insects, which transmit signals back to central receiver(s) at regular intervals	Measures movement at fine spatial and temporal scales	Limited to large insects Expensive, but becoming more affordable as technology improves Antenna may alter insects' behaviour (as it does for birds: Barron et al. 2010)	Cant et al. (2005)
<i>Tracking</i> . Researchers follow individual insects as they move in the landscape, recording distance moved, orientation, timing, etc.	Biologically intuitive measure of movement Measures movement at fine spatial and temporal scales for individual insects	Labour-intensive As with other natural-setting methods, affected by weather and landscape Researchers may affect insect behaviour	Cormont et al. (2011)
<i>Measurements in a controlled setting</i> . Lab- or field-based enclosures in which individuals' movement is tracked	High precision for individual insects Removes external factors (e.g., predation of marked individuals)	Artificial nature of setting may affect behaviour	Field: Saastamoinen (2007); lab: Karlsson and Johansson (2008)
<i>Proxy traits</i> . Use of life-history, morphological, or geographic traits likely to correlate with mobility	Proxy data are easier to obtain than movement data, allowing greater sample sizes and taxonomic breadth	Many proxies fail to correlate strongly with mobility when actually tested (e.g., wingspan vs. mobility in the present study), or covary with additional traits complicating interpretation	Geographic: Beck and Kitching (2007); morphological: Öckinger et al. (2010)

Table 1 continued

Method	Advantages	Limitations	Example
<i>Vagrancy</i> . Mobility estimated based on how often a species is found in unsuitable habitat, and how close the nearest suitable habitat is	Biologically intuitive measure of dispersal Correlates well with other measures of dispersal (Stevens et al. 2010b)	Requires thorough knowledge of species' life histories (larval host plants, adult feeding resources, etc.) as well as plant species composition in the study area Generalization beyond the location of the study requires consideration of landscape factors	Cook et al. (2001)
<i>Expert knowledge</i> . Ask experts to estimate species' mobility (also called expert elicitation)	Fast and inexpensive, allowing large sample sizes Estimates based on a variety of populations, landscapes, and timescales, so generalizable	People can be mistaken Species-scale measure that ignores individual variation Scientists may lack confidence in conducting or interpreting knowledge-based research	Cowley et al. (2001)

Targeted reviews are available for methods of measuring saproxylic insect dispersal (Ranius 2006) and bee foraging ranges (Greenleaf et al. 2007)

Butterfly mobility has been the subject of less research in North America than in Europe, but this does not mean there is a lack of knowledge of North American butterfly mobility. There are many lepidopterists (moths and butterflies represent the order Lepidoptera) in North America—including many amateur lepidopterists—with extensive knowledge of butterfly mobility; their knowledge simply has not frequently been published as formal studies in peer-reviewed journals. Tapping into lepidopterists' first-hand knowledge of butterfly behaviour would allow rapid progress in mobility research for North American butterflies, provided the methods used take into account the challenges inherent in research that relies on people's knowledge.

We had three goals for our research: (1) construct a database of mobility estimates for the butterflies of Canada based on lepidopterists' knowledge; (2) Develop and utilize methods to quantify variation among respondents in knowledge-based ecological research; and (3) Using our database test the hypothesized relationships between mobility and several species-level traits.

We relied on expert knowledge to construct our database. We identified professional and amateur lepidopterists across Canada and northern USA and asked them to estimate the mobility of those species with which they were familiar on a scale of 0–10. Butterflies are unusual among insects in that people generally like them (Kellert 1993), thus many butterfly enthusiasts are available for research dependent upon expert opinion (e.g., 5,000 members of the North American Butterfly Association, many of whom volunteer with monitoring programs, Jeffrey Glassberg, pers. comm.). Four projects have used expert knowledge to obtain mobility estimates for European butterflies (Bink 1992 as cited in Stevens et al. 2010; Cowley et al. 2001; Komonen et al. 2004; Heikkinen et al. 2010), each differing somewhat in their methodology but producing consistent results (consistency between the first three studies is analyzed in Stevens et al. 2010b). Our study differs from these European studies in target taxa (North American as opposed to European butterflies), our larger scale (more respondents, more species, and greater spatial extent), and our development and use of methods to address data accuracy issues that may arise with knowledge-based data (see below).

We developed novel methods to evaluate the influences of respondent expertise and sample size on data agreement and precision. The use of expert knowledge itself is not novel—in fact the use of expert knowledge in ecological research is increasing rapidly (Brook and McLachlan 2008). While other studies have referred to expert knowledge as expert opinion (e.g., Donlan et al. 2010), we suggest there is a subtle but important distinction between knowledge and opinion: knowledge requires lived experience but opinion does not. Biologists may be skeptical of knowledge-based research for the simple reason that people can be wrong. To address this limitation to knowledge-based research, methods must account for data accuracy vulnerabilities, and explain their methodology in greater detail than is often provided in such research (Davis and Wagner 2003; Brook and McLachlan 2008). We have developed methods to investigate the influence of two potential influences upon mobility score variation: respondents' level of expertise, and the number of responses per species. Other research projects that rely on experts' knowledge or data collection by non-scientists (e.g., citizen science, Silvertown 2009) have addressed respondent expertise in ways that range from treating every respondent as equal to eliminating data from respondents who do not meet certain criteria (e.g., discarding crab collection data from young volunteers who did not meet a threshold education level, Delaney et al. 2008). Our methods should contribute to the ongoing improvement of knowledge- and citizen-based science methodology.

We used the mobility data arising from our project to test five biological hypotheses. First, we tested the hypothesis that closely-related species have more similar mobility than distantly-related species (i.e., mobility has a phylogenetic signal). Mobility is the product of several morphological and physiological traits, which themselves can carry a strong phylogenetic signal (Blomberg et al. 2003), so we would expect (but should not assume, Losos 2008) that mobility also carries a phylogenetic signal.

Second, we tested the hypothesis that large butterflies (based on forewing wingspan) are more mobile than small butterflies. Wing length can positively correlate with dispersal among individual butterflies within species (Dockx 2007), and has been used as a proxy for species-level dispersal rates in biogeographic research (Kharouba et al. 2009; Öckinger et al. 2010). For this analysis and other species-level trait comparisons we used phylogenetically explicit analyses whenever possible to account for phylogenetic autocorrelation of data from related species (see “[Materials and methods](#)” section).

Third, we tested the hypothesis that mobile species have larger species ranges than less-mobile species. Lester et al. (2007) summarize three families of hypotheses for why mobile species should have larger ranges. Site colonization hypotheses suggest dispersal limits species’ ability to colonize suitable habitats, leading to smaller ranges for less-mobile species. The speciation rate hypothesis suggests species with limited dispersal have low levels of gene flow, leading to increased rates of speciation between isolated populations. The selection hypothesis suggests there is selection for reduced mobility among species with narrow ranges. The hypotheses are logical, but evidence supporting their shared prediction of mobile species having larger ranges is mixed (Lester et al. 2007).

Fourth, we tested the hypothesis that larval host plant generalist species are more mobile than specialists. Host plant specialists are less likely to be limited by host plant occurrence, reducing the cost of dispersal (Komonen et al. 2004).

Finally, we tested the hypothesis that less-mobile species are at greater conservation risk than highly-mobile species. Sedentary species should be more vulnerable than highly-mobile species to habitat fragmentation and isolation (Kuussaari et al. 2007).

Materials and methods

Butterfly taxa

We used data from the Butterflies of Canada database (Layberry et al. 1998) to determine what species have been found in Canada, and where in Canada they were found. This database contains approximately 300,000 dated, georeferenced records of butterfly collections and observations, dating from the 1800s until present. Based on these data we produced a list of 307 butterfly (superfamily Papilionoidea) and skipper (Hesperioidea) taxa found in Canada, most of which were species and a few subspecies. Collection locations of these taxa were used to determine under which region(s) of Canada the taxa should be listed (see “[Questionnaire](#)” section). Taxonomy follows Warren et al. (2009) for HesperIIDae, and Pelham (2008) for Lycaenidae, Nymphalidae, Papilionidae, Pieridae, and Riodinidae.

Questionnaire

We distributed our questionnaire file electronically to lepidopterists during summer and fall 2009. The questionnaire was distributed by e-mail or by downloads from J.M.F.’s

website, and consisted of a Microsoft Excel file listing species (Supporting File S1) along with the project background and instructions. Questionnaire methods were based largely on those of previous butterfly mobility questionnaires in Britain (Cowley et al. 2001) and Finland (Komonen et al. 2004). Respondents were instructed to enter a mobility score from zero (sedentary) to ten (extremely mobile) for each species with which they were familiar. Six tabs in the spreadsheet listed the species found in five geopolitical regions of Canada (BC & AB; SK & MB; ON & PQ; Atlantic provinces; and northern territories) and the list of all Canadian species. Respondents were asked to consider three questions to help guide their definition of mobility, as used in the Finnish questionnaire (Komonen, pers. comm.): (1) Do butterflies of this species frequently move between patches of habitat, or stay within a patch? (2) Are the individuals frequently taking off or resting for long periods of time? (3) Are the individuals easy to catch or difficult to catch?

We distributed our questionnaire to amateur and professional butterfly enthusiasts across Canada and northern USA, whom we identified in five different ways. First, we sent it to lepidopterists with whom we were familiar and people suggested by these lepidopterists. Second, we sent it to authors of butterfly field research with which we were familiar. Third, we sent it to entomological clubs and societies across Canada, asking them to forward our e-mail to their members, publish our request for assistance in their newsletters, and post the request on their websites. Fourth, we presented this research at two entomological research conferences, asking for volunteers in the audience to contact us for a questionnaire. Finally, we sent the questionnaire to individuals listed as regional butterfly count contact compilers in northern states of the USA on the website of the North American Butterfly Association (www.naba.org/counts/maps08.html), and suggested which Canadian region tab of our questionnaire was closest to their location.

We originally listed only 137 of the most common species in our questionnaire because we wanted to minimize questionnaire complexity in order to maximize response rate (White et al. 2005). Early respondents asked permission to estimate mobility for additional species not included on the list. In response to this feedback we changed the questionnaire to include all Canadian taxa.

We evaluated the influence of the number of mobility estimates for a species upon mobility score consistency. We calculated the absolute difference in species' mean mobility scores as cumulative respondents' scores were added, randomizing the order in which respondents' scores were added using Microsoft Excel 2007. We ran as many respondent order randomizations as there were respondents for a species. For example, 15 respondents rated mobility for *Boloria eunomia*, so we randomized the order of those respondents 15 times, calculating the difference in *B. eunomia*'s mean mobility when using n versus $n - 1$ respondents each time for $n = 2$, $n = 3$, and so on until $n = 15$. Because any average is less sensitive to additional data points as more and more are added, we created a null model to reflect the sensitivity of mean mobility scores to additional random data points. To create this null model, we randomly shuffled mobility scores among species within respondents and calculated mean mobility of pseudo-species based on these randomized mobility scores. This maintained the structure of the data in the null model (e.g., all of Respondent #1's scores remain, but they are now scattered among different species than she had intended). Comparison of the sensitivity curves for actual and randomized (null) mobility scores reveals whether actual mobility means are more or less sensitive to additional data points than are means of random mobility scores.

Respondent expertise

Respondent expertise can influence the reliability and sensitivity of results (Delaney et al. 2008; Fitzpatrick et al. 2009; Donlan et al. 2010), so we included questions in our questionnaire file designed to produce measures of respondents' in-the-field butterfly expertise (Supporting File S1). We asked: (1) self-assessment of expertise on a scale of one to ten, with ten being expert; (2) how frequently they sample butterflies per field season; (3) number of years worked on each species whose mobility they estimated; (4) whether or not they had contributed to a butterfly census; and (5) whether or not they had conducted butterfly ecological research. We consolidated responses to the two latter questions into one continuous variable ("scientific contribution": 0 = no to both, 1 = yes to one, 2 = yes to both questions), because Principal Components Analysis (PCA) requires continuous variables.

Using the four expertise variables listed above along with the number of taxa rated by the respondent as a fifth expertise variable, we calculated a PCA to extract orthogonal variables of expertise using S-Plus version 8.0 (Insightful Corp.). For our response variable against which we compared PCA axes of expertise, we obtained the absolute values of the difference between respondents' mobility estimates for each species and that species' mean mobility score based on all other respondents. These residual scores were averaged for each respondent to give "respondent inconsistency," a value of how different their mobility estimates were from those of all other respondents. If a respondent's mobility estimate for a single species differs from other respondents' estimates, this may reflect the respondent being mistaken, all other respondents being mistaken, or intraspecific variation in the species' mobility. But for a respondent to consistently provide mobility estimates that differ from other respondents across multiple species likely reflects inaccuracy in the respondent's responses (see Lintott et al. 2008 for discussion of weighting respondents by their agreement with others in a citizen-based astronomy project). We performed a general linear regression for overall respondent inconsistency with PCA axes of expertise as predictor variables in JMP version 8.0.2 (SAS Institute Inc.). Results did not suggest any relationship between expertise and respondent inconsistency (see "Results" section). If we had found such a relationship then we would have either set a threshold of expertise below which we discounted respondents (e.g., van Swaay et al. 2006; Delaney et al. 2008) or weighted mobility estimates by expertise or consistency, depending on the nature of the respondent inconsistency–expertise relationship.

Phylogenetic tree

We constructed two phylogenetic trees for our species: a DNA-based tree and an all-species tree. The DNA-based tree included 78 species with mobility estimates for which DNA sequences of any of three genes were available in Genbank (*EF-1 α* , *wingless*, and *COI*). We constructed a consensus tree based on these sequence data using MrBayes version 3.1.2 with default settings (Ronquist and Huelsenbeck 2003). We ran the Bayesian analysis until the average standard deviation of split frequencies fell consistently below 0.005, which took 30,000,000 generations. For outgroups we used Genbank sequences for two moth species: *Archiearis parthenias* (family Geometridae) and *Urania leilia* (Ura-niidae). We used this DNA-based tree (Supporting File S2) to test for a phylogenetic signal in mobility estimates. The all-species tree (Fig. S1) used the DNA-based tree as a foundation, with all additional species added onto the tree following a set of rules based on

taxonomic affiliations (Fig. S2) using Mesquite version 2.72 (Maddison and Maddison 2009). We used the all-species tree to account for phylogenetic autocorrelation in analyses of the relationship between mobility and traits (see below). Given the common reality of data limitations for tree construction, phylogenetic researchers recommend using simplistic trees rather than not accounting for phylogenetic autocorrelation at all (Purvis 2008), and studies have found that phylogenetic analyses are robust to reasonable variation in tree structure (Cadotte et al. 2009). Our trees resemble those for mostly non-Canadian species produced using more taxa, sequences, and characters than ours (Wahlberg et al. 2005; Mutanen et al. 2010). The two phylogenetic results that do not match previous findings are: (1) *Speyeria mormonia* did not cluster with congeneric taxa and (2) *Danaus plexippus* did not cluster with its fellow nymphalid butterflies.

Phylogenetic signal

To test for phylogenetic signal in mobility we used the REGRESSIONv2.m program (Lavin et al. 2008) in Matlab version 7.0.4.365 (MathWorks Inc.) to determine which of the following models of evolution best fit the data: ordinary least squares (OLS, a star-shaped phylogeny corresponding to no phylogenetic signal), generalized least squares (GLS) with Brownian motion, GLS with Ornstein-Uhlenbeck (OU) transformation, GLS with Accelerating-Decelerating (ACDC) transformation, and GLS with Pagel's λ transformation. Another model of evolution, GLS with Grafen's ρ transformation, could not be computed. Each of the GLS transformations makes different assumptions about evolutionary constraints and processes, and each should be considered to determine which evolutionary model fits the data best (Garland et al. 2005). The fit of each model to mobility data was measured with Akaike's Information Criterion (AIC) scores, from which evidence ratios were calculated to produce results with intuitive interpretation (e.g., model A is three times more likely than model B given the data) (Garamszegi et al. 2009).

Trait data

Average wingspan data (distance between tips of forewings in mm, obtained from Layberry et al. 1998) were transformed using the Box-Cox procedure in JMP ($\lambda = -0.6$) to improve normality.

We obtained North American (north of Mexico) range size estimates from the distribution maps in Scott (1986). Distribution maps were scanned and projected onto a North American grid using ArcGIS software (ESRI) in order to calculate range size (km²) for each species. Range size data were transformed using the Box-Cox procedure ($\lambda = 0.4$) to produce normality.

Larval host plant breadth data were obtained from Layberry et al. (1998), with species being classified as monophagous (one host species), oligophagous (congeneric host species), or polyphagous (host species in more than one genus). Wingspan and larval host plant breadth data were also obtained from another source (Opler et al. 2010), but results were similar so only results using data from Layberry et al. (1998) are reported.

Global conservation status data were obtained from NatureServe (2009), with low values representing threatened species and high values representing species of no conservation concern. When conservation status was given as a range, representing uncertainty in status, we used the lowest value of the range.

Trait analyses

When testing the relationships between traits and mobility, we accounted for phylogenetic autocorrelation among species. The assumption of independent data is violated when species share evolutionary history, necessitating methods such as phylogenetic independent contrasts (ICs) to eliminate pseudoreplication and reduce both Type I and Type II errors (Garland et al. 2005; Purvis 2008). We used PDAP module version 1.14 (Midford et al. 2003) within the Mesquite environment to calculate IC values for the relationships of mobility versus wingspan and mobility versus range size, based on our all-species tree with branch lengths. ICs assume Brownian motion evolution. We standardized raw IC values by dividing them by standard deviations (square roots of the sums of branch lengths).

We calculated Pearson product-moment correlations between ICs of mobility and both wingspan and range size in PDAP. Because there are numerous soft polytomies in our phylogenetic tree (i.e., nodes with multiple branches without resolution among them), Type I error rates of statistical analyses could be slightly inflated unless we reduced our degrees of freedom (Garland and Díaz-Uriarte 1999). We thus followed the conservative approach described by Purvis and Garland (1993), using the number of nodes in our tree minus one as our degrees of freedom (129 non-outgroup nodes $- 1 = 128$) rather than the more liberal degrees of freedom based on 291 taxa to determine significance.

We calculated the relationship between mobility (response) and larval host plant breadth (categorical predictor) in a general linear model using REGRESSIONv2.m. We compared the AIC values for this relationship under four phylogenetic assumptions described in our test for phylogenetic signal, reporting results from the model with the lowest AIC value: OLS (no phylogeny), GLS (Brownian), GLS (OU), and GLS (Pagel's λ) (GLS (ACDC) could not be computed for this analysis).

We calculated the relationship between conservation status (ordinal response) and mobility (continuous predictor) in a multinomial ordinal regression using JMP. We were not aware of a method to account for phylogenetic autocorrelation with multinomial ordinal regression, so we used raw trait values. To determine whether our inability to account for phylogenetic autocorrelation may have affected results, we also calculated the relationship between conservation status and mobility in logistic regression models with and without phylogenetic autocorrelation, comparing the results of both analyses. To do so we re-classified conservation status as a binary variable, grouping status values 1–3 and 4–5. We used the PLogReg.m (Ives and Garland 2010) program in Matlab, comparing logistic regression with Firth correction without phylogenetic methods versus with phylogenetic methods. We determined that phylogenetic methods did not strongly influence the coefficient for mobility obtained from quasi-likelihood estimation (-0.98 ± 0.19 without phylogenetic methods vs. -0.97 ± 0.32 with phylogenetic methods). Therefore, we are confident that our multinomial ordinal regression for the influence of mobility on conservation status was not affected by our inability to account for phylogenetic autocorrelation.

To control for inflated Type I error associated with multiple hypothesis tests, we used the classical one-stage method Benjamini–Hochberg procedure to control the false discovery rate (FDR) (Benjamini and Hochberg 1995). For each of six significance tests we report the P -value and whether this value is less than or greater than the FDR-adjusted significance threshold for that test (e.g., of non-significance: $P = 0.030 > \alpha_{\text{FDR}} = 0.025$). With our alpha value of 0.05, this means that 5% of our post-FDR significant results can be expected to be the result of chance alone (Waite and Campbell 2006). This notation for significance thresholds is unconventional (see Pike 2011 for other notation), but we believe it is more transparent to readers than FDR-adjusted P -values.

Results

Questionnaire respondents

Fifty-one lepidopterists completed questionnaires, representing all regions of Canada (Table S1). Together our respondents represent approximately 788 years of butterfly experience, based on the longest time respondents had spent working on butterflies, averaged across respondents who provided such information (mean = 15.5 years, $n = 40$) and extrapolated to respondents who did not provide estimates of years of experience ($n = 11$). It is impossible to calculate a response rate since our questionnaire was distributed not only by direct invitations to individuals but also passively through newsletters, conferences, and internet links.

Expertise

The first two PCA axes explained 39 and 23% of the variation in the expertise variables, respectively, for a total of 62%. One respondent was excluded from expertise PCA analyses because her data strongly skewed results (note her mobility data were not excluded). She is conducting intensive field research on a rare butterfly species, which is why we encouraged her to provide us with mobility estimates. On the one hand she could be considered a novice because she rated her own expertise as low, rated few species' mobility, and had only a few years' experience with butterflies, but on the other hand she sampled butterflies far more frequently per field season than any other respondent, skewing PCA axis loadings considerably. A linear regression with both PCA axes did not explain significant variation in respondent inconsistency ($F_{2, 31} = 0.4362$, $P = 0.651 > \alpha_{\text{FDR}} = 0.05$), eliminating the need to set a threshold of expertise below which we discounted respondents or weight mobility estimates by expertise.

Mobility: number of respondents

We received mobility estimates for 291 out of the 307 taxa known to inhabit Canada (Supplementary File S3). Most species received a small number of mobility estimates, with only a few species being rated by almost all respondents, and a median of seven mobility estimates per species (Fig. S3). Widespread species received more mobility estimates than species with narrow ranges (Pearson correlation of phylogenetic contrasts between North American range size and number of respondents: $n = 229$, $df = 128$, $r^2 = 0.52$, $P < 0.0001 < \alpha_{\text{FDR}} = 0.0083$). Both the actual and randomized mobility means for species changed less with each subsequent mobility estimate, as predicted, with actual means being less sensitive than randomized means to additional data points (Fig. 1).

Mobility: distribution

Mean mobility followed an approximately normal distribution, with most species having intermediate values (Fig. 2). The standard deviation of mobility scores around each species' mean indicates some combination of uncertainty and real intraspecific variation (Kuhnert et al. 2010). Standard deviation values were higher for species with intermediate mobility scores than for either sedentary or highly-mobile species (Fig. S4), indicating greater consensus among respondents for mobility of the most sedentary and most mobile species than for somewhat-mobile species.

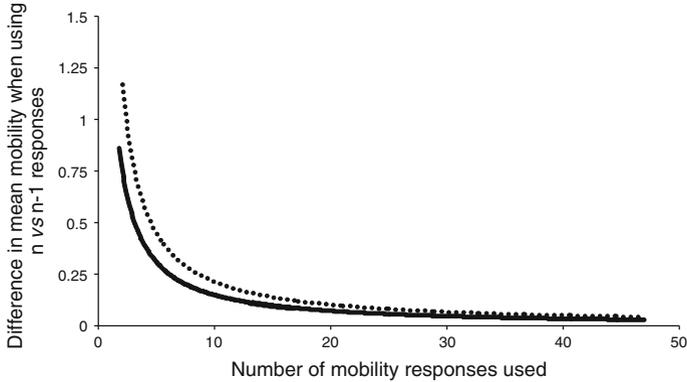
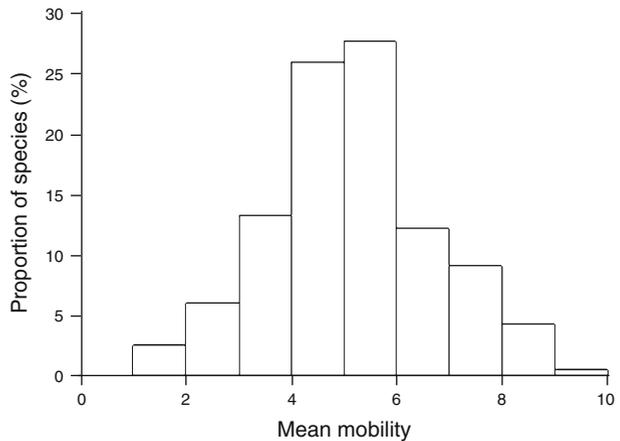


Fig. 1 Effect of cumulative mobility responses on species' mean mobility scores. The effect of incorporating additional respondents' mobility estimates on average mobility values were calculated using actual species' mobility estimates (*solid line*) and a null model based on a random mix of species' mobility estimates (*dotted line*) (see “[Materials and methods](#)” section for details)

Fig. 2 Proportion of species with various mean mobility estimates



Phylogenetic signal

Mobility displayed a strong phylogenetic signal, being more similar among closely- than distantly-related taxa. The evolutionary model with Pagel's λ transformation ($\lambda = 0.92$) was 48 times more likely than the next-best evolutionary model (OU transformation) given the data, and more than 1,000 times more likely than the scenario in which evolutionary history does not affect mobility (Table 2).

Traits

There was a positive but weak correlation between wingspan and mobility (correlation of phylogenetic contrasts: $n = 277$, $df = 128$, $r^2 = 0.05$, $P = 0.0004 < \alpha_{FDR} = 0.0417$; Fig. 3). Species range size was positively correlated with mobility (correlation of

Table 2 Results of tests for phylogenetic signal in species’ mean mobility scores

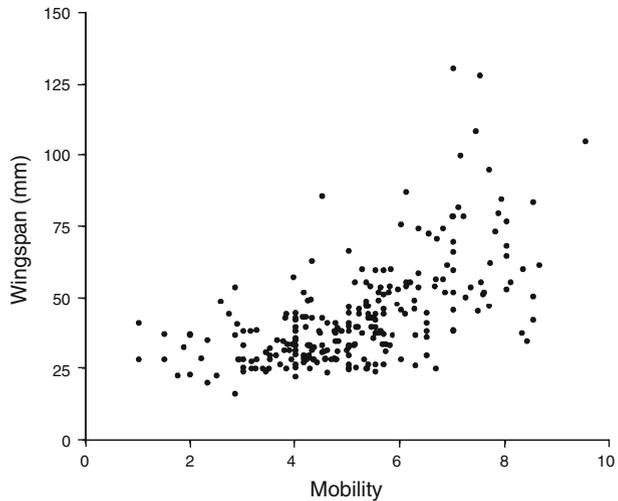
Model	Transformation estimate ^a	AIC	Δ AIC ^b	Evidence ratio ^c
GLS (λ)	0.92	231.9	0	1
GLS (OU)	0.68	239.7	7.7	48
GLS (Brownian)	–	256.6	24.7	>10 ³
GLS (ACDC)	0.92	257.7	25.7	>10 ³
OLS	–	274.6	42.7	>10 ³

^a Transformation values can be considered the effect size of the evolutionary rate transformation, with zero representing no influence of evolutionary history and one the amount of niche conservatism expected from Brownian motion (for details see Lavin et al. 2008)

^b Difference in AIC between the best-ranked (lowest AIC) model and the given model

^c Model weight of the first-ranked model relative to that of the given model. Interpreted as how much more likely the best-ranked model is than a given model (an approximation based on large sample size conditions)

Fig. 3 Relationship between species’ mean mobility and wingspan ($n = 278$). This figure displays untransformed raw data without phylogenetically ICs to give readers a sense of the data



phylogenetic contrasts: $n = 229$, $df = 128$, $r^2 = 0.15$, $P < 0.0001 < \alpha_{FDR} = 0.0167$; Fig. 4).

Mobility differed between larval host plant specificity categories ($F_{2, 260} = 9.31$, $P = 0.0001 < \alpha_{FDR} = 0.0333$), with polyphagous species being more mobile than either monophagous or oligophagous species (Fig. 5). The ANOVA model with Pagel’s λ transformation ($\lambda = 0.78$, $R^2 = 0.07$) was more than 1,000 times more likely given the data than the OLS ANOVA that ignored phylogenetic autocorrelation.

Mobility significantly influenced conservation status (equivalent $R^2(U) = 0.10$, $X^2_{1, 285} = 43.89$, $P < 0.0001 < \alpha_{FDR} = 0.025$), with sedentary species being most at-risk (Fig. 6).

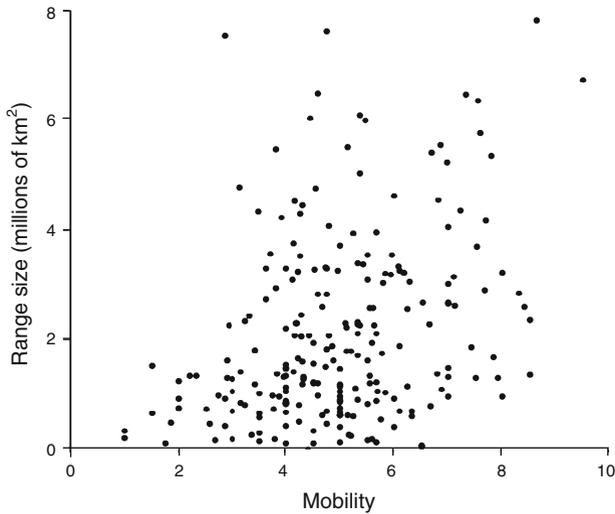


Fig. 4 Relationship between species' mean mobility and North American range size ($n = 230$). This figure displays untransformed raw data without phylogenetically ICs to give readers a sense of the data

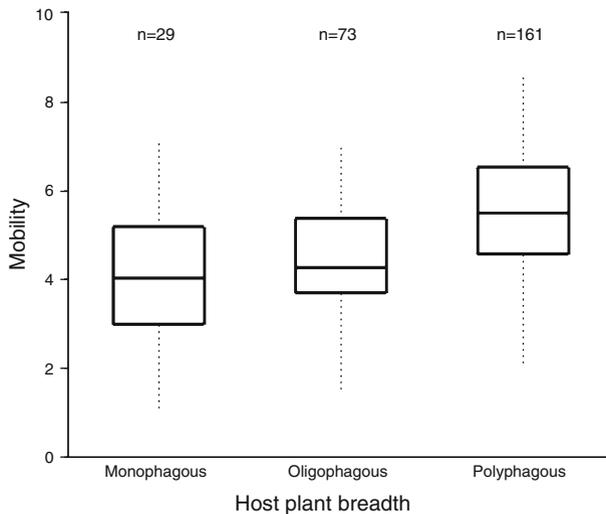


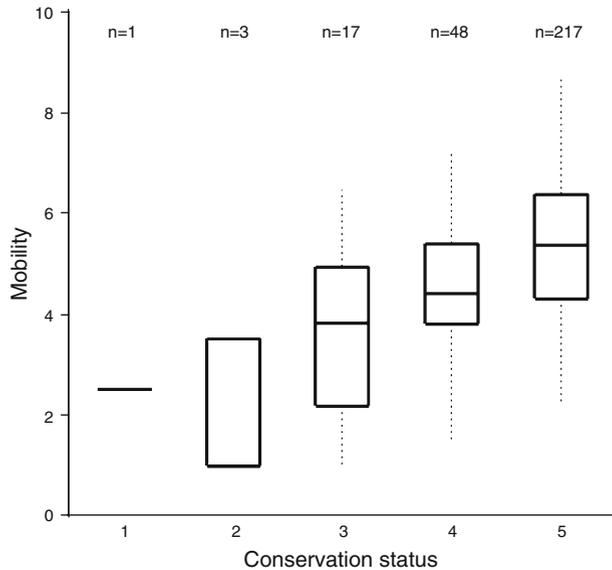
Fig. 5 Mean mobility of species of different larval host plant breadth (monophagous species are host plant specialists, polyphagous are generalists). Ends of the *box* represent the 25th and 75th quantiles, the *mid-line* represents the median, and *whiskers* extend to the 10th and 90th percentiles. Sample sizes for each breadth category are indicated above *box plots*. Raw data are displayed without phylogenetic transformation

Discussion

Data set

In 6 months we obtained mobility estimates for 95% of the butterfly species in Canada (291 out of 307 taxa), relying on approximately 800 years of expertise accumulated among

Fig. 6 Mean mobility of species of different conservation status, with lower numbers representing species at greater conservation risk. Ends of the *box* represent the 25th and 75th quantiles, the *mid-line* represents the median, and *whiskers* extend to the 10th and 90th percentiles. Sample sizes for each conservation category are indicated above *box plots*. Analysis used conservation status as the response variable, but mobility is displayed on the y-axis for ease of interpretation



51 lepidopterist respondents. Because mobility is an important biological trait, and butterflies are often used as a model taxonomic group, we anticipate these data will allow investigations into both basic biology and applied conservation not previously possible. For example, our data should assist decisions on what species are candidates for assisted colonization. Sedentary species are considered vulnerable to the combined effects of climate change and habitat fragmentation since they are unlikely to fly over inhospitable matrix habitat (e.g., farms) to colonize new sites at cooler latitudes (Hoegh-Guldberg et al. 2008; Thomas et al. 2011). Experimental translocations of butterflies to habitats farther north than their range margin have been successful in the UK, suggesting some species' range expansions are dispersal-limited (Willis et al. 2009). Whether and how we should proceed with assisted colonization for North American butterflies is beyond the scope of this paper (for debate see Hoegh-Guldberg et al. 2008; Ricciardi and Simberloff 2009), but such decisions depend on understanding species' mobility behaviour.

Methods for knowledge-based ecology

We found no evidence of respondents' expertise influencing results, and the influence of sample size upon mean mobility scores was fairly small. There was remarkable consistency among respondents' mobility scores for species, with greater consistency for sedentary and highly-mobile species than for somewhat-mobile species. Respondent expertise did not explain any variation in respondent inconsistency. This is likely due to low variation in both respondent inconsistency and respondent expertise. We targeted butterfly experts, and even among people we considered experts (based on the same criteria used to determine expertise in this study) many declined to complete the survey because they felt they did not know enough about butterflies, suggesting a high level of expertise among respondents. We calculated standard deviations in mobility scores for each species, and calculated the general trend of the influence of sample size upon species' mean mobility scores. We have chosen to present these data and to refrain from recommending a minimum sample size

below which mobility estimates should be ignored, because different researchers will require different levels of confidence in data depending on their purpose. These variation data may also be used as estimates of uncertainty in Bayesian analyses (Kuhnert et al. 2010).

Knowledge-based research poses several challenges. Experts can be wrong, such as errors in expert testimony among forensic scientists (Saks and Koehler 2005). Knowledge-based research should therefore include assessment of inter-rater agreement (Davis and Wagner 2003; Brook and McLachlan 2008) and data accuracy (e.g., Delaney et al. 2008; Sullivan et al. 2009). More and more projects are relying on data contributed by non-scientists (Brook and McLachlan 2008; Silvertown 2009), so the importance of methods related to data accuracy checks among diverse data contributors should increase in the future. Local ecological knowledge (LEK) is one type of research dependent on non-scientists' knowledge, whereby people with relevant local experience provide their understanding of ecological matters (Brook and McLachlan 2008). For example, Anadón et al. (2009) employed LEK by asking shepherds to estimate the number of tortoises they saw on pasture land. Citizen science, like LEK, is increasing in frequency rapidly and generally involves citizens contributing data to projects managed by scientists (Silvertown 2009). For example, citizens voluntarily contribute bird sightings to the Cornell Lab of Ornithology's numerous bird monitoring projects (Bonney et al. 2009). Citizen science projects often ask for quantitative data (e.g., the number and species of birds visiting your backyard bird feeder), but these data can still be subjective (e.g., I think those two birds were Song Sparrows because I recognized their call). The boundaries distinguishing expert knowledge, LEK, and citizen science are somewhat blurry. Their boundaries, and more challenging boundaries such as the line between a data contributor and a project author, will likely blur more as continued improvements in digital information sharing technology 'democratize' science, allowing greater participation of amateur scientists in scientific research (Marshall 2008; Stodden 2010). If appropriate methods are followed, knowledge-based research can provide immense quantities of reliable data quickly, cost-effectively, and based on many years of direct experience as we found in our project. 'Crowdsourcing' methods have been used successfully not only in biodiversity monitoring programs (Devictor et al. 2010), but also in other diverse areas of ecological and evolutionary research (Table S2). A diversity of research approaches, rather than devotion to any one approach, benefits the science of biology (Weber 1999).

Butterfly mobility

We found that, like most ecological traits (Freckleton et al. 2002), mobility has a phylogenetic signal. This is not surprising, given that mobility depends on several morphological and physiological traits, which tend to have a phylogenetic signal themselves (Blomberg et al. 2003). Our estimate of signal may be inflated as a result of closely related species being listed on nearby rows in our questionnaire (species were listed alphabetically by Latin name within families), potentially allowing respondents to use their estimates for one species as a basis for closely related species in subsequent rows. A previous study of European butterflies found phylogenetic signal for direct measures of dispersal ability, but no signal for indirect (genetic) measures of dispersal (Stevens et al. 2010a).

Wingspan has been used as a proxy for butterfly mobility (Kharouba et al. 2009; Öckinger et al. 2010), but we found only a weak relationship between them once phylogeny was accounted for. Neither Kharouba et al. (2009) nor Öckinger et al. (2010) used phylogenetically explicit analyses, so we investigated the influence of phylogenetic

methods on the correlation between wingspan and mobility. When we calculated a simple correlation with our raw data we found a positive correlation between mobility and log-transformed wingspan ($n = 279$, $r^2 = 0.36$, $P < 0.0001$), which is stronger than the correlation reported by Öckinger et al. (2010) between European species' wingspan and expert knowledge derived mobility estimates ($n = 123$, $r^2 = 0.09$, $P < 0.001$). We conclude that the correlation between wingspan and mobility is mostly indistinguishable from phylogenetic similarity, so the greater mobility of large butterflies may be due to their wingspan or to other evolved traits. Wingspan may be a valid proxy for mobility in taxa where brachypterous (short-winged) species fly and disperse less than macropterous (long-winged) species (Gutiérrez and Menéndez 1997; but see Hendrickx et al. 2009), but it seems to be at best a weak proxy for mobility in Lepidoptera (our results and those of Beck and Kitching 2007; Betzholtz and Franzen 2011). Other morphological traits have the potential to be more representative of mobility such as thorax to abdomen volume ratio, wing loading, aspect ratio, and wing shape (Wickman 1992; Dudley and Srygley 1994; Altizer and Davis 2010). Access to wing morphology traits is improving with online databanks of butterfly images including museum collections' images (e.g., www.nhm.ac.uk/research-curation/research/projects/cockayne/index.html), databases such as www.morphbank.net, and potential future automation of character recognition and measurement (La Salle et al. 2009).

Mobile species have larger ranges than sedentary species, as predicted. Among Lepidoptera, mobile species generally have larger ranges (Cowley et al. 2001; Dennis et al. 2005; Beck and Kitching 2007; Betzholtz and Franzen 2011; but see Garcia-Barros and Benito 2010). It seems that the relationship between mobility and range size varies among taxa and regions (Lester et al. 2007), but is positive for Canadian butterflies.

We found host plant generalist species to be more mobile than specialist species. This result supports the argument that host plant generalists are more mobile than specialists because they have a lower cost to dispersal, being more likely to encounter suitable host plants for colonization (Komonen et al. 2004). We propose, however, that although host plant breadth may be related to mobility in some taxa, the explanation supporting this relationship may be overly simplistic for two reasons. First, not only the costs but also the benefits of dispersal should be greater for host plant specialists than for generalists. When a specialist's primary food source becomes rare, it may be more beneficial to disperse to another habitat in search of this resource than to stay in the habitat and forage on secondary food resources inefficiently, but generalists have no such pressure to disperse (e.g., Ter-raube et al. 2011). Second, while the cost of dispersal may be smaller for host plant generalists than specialists, their difference in costs may be less than is commonly assumed because individuals are often more specialized than species. Species that are considered to be host plant generalists may have considerable intraspecific variation such that individuals and populations specialize on host plant species (Fox and Morrow 1981), resulting in a narrower range of colonization opportunities than may be predicted from the species' trait. Populations can have lower realized breadth than the species (e.g., *Mitoura gryneus* butterflies tend to prefer whichever host plant species is sympatric with their population, Downey and Nice, in press), and individuals can have lower realized breadth than the population (e.g., brush mice disperse into the same habitat type as the one in which they were raised, Mabry and Stamps 2008). In addition to individuals' specialization, spatial and temporal variation in plant species' availability may limit colonization to a subset of host plants in the generalist's repertoire (Fox and Morrow 1981). For these reasons, we hypothesize that colonization opportunities may be less abundant than previously assumed for host plant generalists, and thus generalists' cost to dispersal may be greater than previously assumed. We note that this hypothesis is speculative and would require further

research, and further note that the relationship we found between mobility and host plant breadth stands alone from our speculation on the underlying mechanism for the relationship. There are also potential biases in Lepidoptera host plant record data that may affect analyses of host plant breadth (Beck et al. 2006).

If this more complicated relationship between host plant specialization and dispersal is correct, then it is difficult to predict whether specialists or generalists should be more mobile. Previous evidence for Lepidoptera suggests generalists may be more mobile, but the evidence is not strong. Beck and Kitching (2007) found generalist sphingid moths to disperse more than specialists, but they recognized that this result may be an artefact of their proxy for dispersal being island colonization, since colonization is not only a function of dispersal but also niche breadth. Betzholtz and Franzen (2011) found generalist noctuid moths to be more mobile than specialists, with large-range generalists being especially mobile. Both Komonen et al. (2004) and our study found host plant generalists were more mobile than specialists while accounting for phylogenetic autocorrelation, but the strength of the relationship differed between studies, being weaker in our study with a larger sample size.

We found sedentary species to be at greater conservation risk than mobile species. Previous studies in Europe have found similar results (Kotiaho et al. 2005; Wenzel et al. 2006; Kuussaari et al. 2007), but have been criticized for not accounting for phylogenetic autocorrelation (Nylin and Bergström 2009). Unlike Thomas' study of British butterflies (2000), species with intermediate mobility were not at greatest risk, perhaps reflecting the different land use histories of Canada and Britain.

The conservation risk to sedentary species is escalating with increasing habitat fragmentation and climate change. Habitat fragmentation increases isolation between populations, which can reduce rates of colonization in metapopulation dynamics (Wilson et al. 2009). Habitat fragmentation can also selectively exclude sedentary and habitat specialist species from landscapes, resulting in biotic homogenization of remaining habitat with a small number of successful mobile generalists (Ekroos et al. 2010). Climate change is shifting species' climatic envelopes poleward in latitude and upward in elevation (Parmesan and Yohe 2003). Mobile species are better able to expand their latitudinal range than are sedentary species (Pöyry et al. 2009), while species' lower-latitude edge should retreat poleward as warm-adapted mobile competitors invade from lower latitudes (Ackery 2003). Climate change should thus shrink most species' equatorial range boundary, but also restrict sedentary species' capacity to expand poleward (Franco et al. 2006). Note that mobility may be less influential to tropical species' responses to climate change than to temperate species' for three reasons. First, latitudinal temperature gradients are much shallower in the tropics (Colwell et al. 2008), and many tropical species' latitudinal ranges are limited by factors other than temperature (e.g., precipitation: Martin et al. 2009). Second, uphill shifts in elevation are possible in tropical and temperate regions alike (Thomas 2010), but require only short-distance colonization of which most species should be capable (Colwell et al. 2008). Because mountains have less area at higher elevations, species will be in greater competition for resources as they shift uphill, which could in fact select against mobility if there is a trade-off between species' mobility and competitive ability (Hendrickx et al. 2009). Third, although tropical latitudes are warming less rapidly than temperate latitudes, tropical ectotherms have a narrower thermal tolerance than temperate species so conservation risk may be influenced by physiological traits (Deutsch et al. 2008; Dillon et al. 2010).

We intended to test the relationship between mobility and an additional trait, genome size, but only three species in our data set have genome size estimates so formal tests were not possible. Genome size is known to relate to species' flight capacity in Odonata

(dragonflies and damselflies), with species that fly in short powerful bursts having small genomes (Ardila-Garcia and Gregory 2009). It is noteworthy that the species with the highest mobility score in our data set (the Monarch) has the smallest genome of any of the more than 50 species of Lepidoptera yet quantified (Gregory and Hebert 2003).

Future directions, conclusion

Incorporating dispersal estimates into models of species' responses to habitat or climate change may improve the accuracy of their outputs. Ecological niche modelling, for example, is used to predict species' distributions in response to climate change and potential ranges of invasive species (Wiens et al. 2009). One of the main limitations of these models is they generally assume species have either no or infinite dispersal capacity, which hinders their ability to predict range shifts over time. Incorporating dispersal into ecological niche modelling may improve conservation planning (Engler and Guisan 2009).

Our research focused on mobility variation between species, but it is important to keep in mind that individuals' mobility depends on many intrinsic (e.g., body condition) and extrinsic (e.g., weather) factors (Bowler and Benton 2005). Intraspecific variation in butterfly mobility (Stevens et al. 2010a) and mobility-related wing morphology (Cassel-Lundhagen et al. 2009; Gibbs et al. 2011) can be considerable. Intraspecific variation in dispersal ability can be great when comparing individuals from the expanding frontier of a species' range to those from its core (Llewelyn et al. 2010).

The decline of natural history as an integral component of ecological science is well-documented (Dayton 2003; Greene 2005). It can be difficult to quantify natural history characteristics, such as mobility, for large taxonomic groups. Yet, experts, who need not be practicing academics, can convey consistent biological knowledge for groups like butterflies. These naturalists, whatever their background, are often eager to share their knowledge if asked.

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