

Towards a vertebrate demographic data bank

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Abstract The development of computers, appropriate statistical methodology and specialized software has induced an explosion in empirical research on vertebrate population dynamics. Many long-term programs have led to impressive datasets and to the publication of hundreds of estimates of vital rates critical to many areas of ecology: evolution of life history strategies, conservation biology, behavioral ecology, population management, etc. Such estimates are still usually available through regular scientific articles, and their use for comparative purposes suffers from several shortcomings: duplication of technical work, lack of evaluation of methodological bias, and difficulties in linking vital rates estimates with other basic traits such as body size. It thus seems it is time to propose a demographic databank to collect the information on vertebrate demography published and being published and make it widely available. The resulting database should become the equivalent for vertebrate demography to what “Genbank” is for DNA sequences. Bird demography has a critical mass of knowledge adequate for a first step. This paper reviews, based on a prototype database, the outline of such a project of demographic database: type of data and estimates stored, assessment of methodology and data quality, data

documentation, taxonomical and phylogenetical information, link with other existing biodiversity databases, procedures for depositing information, links with scientific journals, etc. The contours of a collaborative group to launch such a project are also discussed.

Keywords Population dynamics · Demography · Comparative approach · Databases · Vertebrates

Introduction

In the general move in ecology from pattern to process (Swihart et al. 2002), population dynamics has evolved from descriptive approaches based on surveys of population size and centered on stability, growth or decrease, to a general emphasis on mechanisms. Flows of individuals, resulting from birth, immigration, death and emigration are estimated, and their consequences on growth regimes are investigated using mathematical models (Caswell 2001) and used to understand population change. This emphasis on mechanisms is now central both to evolutionary ecology (with, e.g., ESS models; Holt 1985) and conservation biology (Beissinger and McCullough 2002). This approach leads to the consideration of demographic parameters (or “vital rates”), such as age-specific annual survival probabilities, as life-history traits of special interest. The availability of reliable estimates of these parameters is obviously critical.

In parallel, the development of computers, appropriate statistical methodology and specialized software, in which the Euring series of conferences has played a major role, has induced an explosion in empirical research on demographic parameters in animal populations, in particular vertebrate populations. Many long-term programs using

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individual marking (Perrins et al. 1991) have led to impressive datasets, some of which have more than 100,000 marked individuals (Cooke et al. 1995). These developments have led to the publication of hundreds of estimates of vital rates (Seber and Schwarz 2002) critical to many areas of ecology: evolution of life history strategies, conservation biology, behavioral ecology, population management, etc. Demographic parameter estimates will become increasingly useful in the context of climatic change, both to assess the degree of susceptibility to extinction and to predict changes in distribution using life-history trait-based models as currently done for trees (Morin et al. 2008) rather than based only on habitat characteristics (e.g., Durner et al. 2009).

Such estimates are still usually available to the scientific community through regular scientific articles, i.e. as disseminated data. However, even in a case study of a single species, difficulties arise. For instance, several estimates of the annual adult survival probability are available. Do they differ because they were obtained in different populations? At different times? By different field or statistical methods? Or with different precisions as a consequence of different sample sizes? The use of published estimates for comparative purposes over a wide range of species also suffers from severe shortcomings: duplication of technical work, heterogeneity of parameter definitions, lack of evaluation of biases, difficulties in linking vital rates estimates with other basic traits such as body size, potential biases in key environmental variables selection, etc.

It thus seems it is time to propose a demographic databank to collect the information on vertebrate demography, published and being published, and make it widely and publicly available (for a similar plea, see Pärtel 2006). The resulting database should become the equivalent for vertebrate demography to what “Genbank” (Benson et al. 2008) is for nucleic acid sequences. Bird demography has a critical mass of knowledge adequate for a first step towards such a database, in particular through the activity of scientists attending the EURING conferences. Out of 445 biodiversity monitoring schemes in the European network “Eumon”, covering both plants and animals, 66% were based on counts, and only 13% included potentially useful demographic information (capture–recapture or age structure data). Birds, with 165 monitoring schemes, were by far the most intensively followed group (<http://www.eumon.ckff.si/biomat/1.1.2.php>). The life cycle of birds is homogeneous enough to fit a fairly standard and common matrix model framework (Lebreton and Clobert 1991; McDonald and Caswell 1993). A few specific cases such as the large biennially breeding albatrosses require some adaptations of the general model (Caswell, personal communication). One should also note that population studies of birds (Lack 1966) have played a key role in the move from pattern to process in population

dynamics and ecology. Mammals are also the subject of intensive population dynamics research with a similar focus on evolutionary (Gaillard et al. 1994) and conservation biology, and an extensive use of comparative approaches (Gaillard et al. 2005). They would be the next logical step towards a vertebrate databank. Other vertebrate groups have received similar, less intense attention (Clobert et al. 1998; Schmidt et al. 2002) and could in turn be considered in such a project.

The purpose of this paper is thus to review, based on a rough prototype database and two illustrative and provisional examples of data use, the contours of such a project of demographic database, with a focus on birds: type of data and estimates stored, assessment of methodology, taxonomical references, link with other existing biodiversity and demographic databases, procedures for depositing information, links with scientific journals, etc. The steps of a collaborative international project are discussed.

A prototype demographic database

The BIRD Demographic Database (BIDDABA (<http://www.cefe.cnrs.fr/BDD/BIDDABA.htm>)) was built by one of us (S.D.) based on a retrospective literature search in limited time (approximately 6 months), which covered 1,016 references, up to 2007. The literature search focused on the EURING conference proceedings and major journals, in particular those easily accessible from the web (such as the American ornithological journals via “Sora” <http://www.library.unm.edu/sora/>), and was centered in priority on papers presenting survival estimates (see Table 1).

The database has been developed in Microsoft Access. Entering or extracting data thus benefit from the Structured Query Language (SQL), although specific user-friendly tools have not yet been developed. As is natural for such a database, each parameter estimate is simultaneously attached to a taxon (species, sometimes with subspecies mentioned), a site (sometimes “NA” = non-available), and a literature reference. Sites, species and references are organized in separate tables. The records in tables of demographic estimates are connected (Fig. 1) to these separate tables by “1 → n” relationships (Ceri et al. 1991). The same type of structure is commonly used, for instance, in the “Global Population Dynamics Database” (GPDD) developed at Imperial College (<http://www3.imperial.ac.uk/cpb/research/patternsandprocesses/gpdd>) and centered on series of population size estimates. The species list can be linked to databases providing information on phylogenetic relationships, such as “the tree of life” (birds: <http://www.tolweb.org/Neornithes>). Similarly, the sites can be linked to a GIS using their geographical coordinates, and to environmental covariates data.

Table 1 The fields of the table of survival estimates in the prototype of the bird demographic database BIDDABA

| Field | Values |
|----------------------------------|---|
| Number | Integer |
| Estimate of survival probability | Numerical $\in [0, 1]$ |
| Standard error of estimate | Numerical |
| Age beginning | Numerical (0, 1, 2, ...) or "a" (for "adult") |
| Age ending | Numerical (0, 1, 2, ...) or "a" (for "adult") |
| Sex | M, F, MF, (mixture), NA (non-available) |
| Method | 1, 2, or 3 (see Table 2) |
| Source: review (vs. paper) | YES or NO |
| Presence of temporal variation | YES or NO |
| Remarks | E.g., "Breeder", "under hunting", "unpublished", etc. |
| Site | Pointer to site table (see Fig. 1) |
| Species | Pointer to species table (see Fig. 1) |
| Reference | Pointer to reference table (see Fig. 1) |

Similar databases on birds and/or mammals have been assembled by various people (e.g., Beissinger 2000; Morgan Ernest 2003; Bielby et al. 2007; etc.). Another noticeable base is the Biodemographic database developed by Vaupel and colleagues at the "Max Planck Institute for Demographic Research" in Rostock (<http://www.demogr.mpg.de/en/research/744.htm>), largely centered on the role

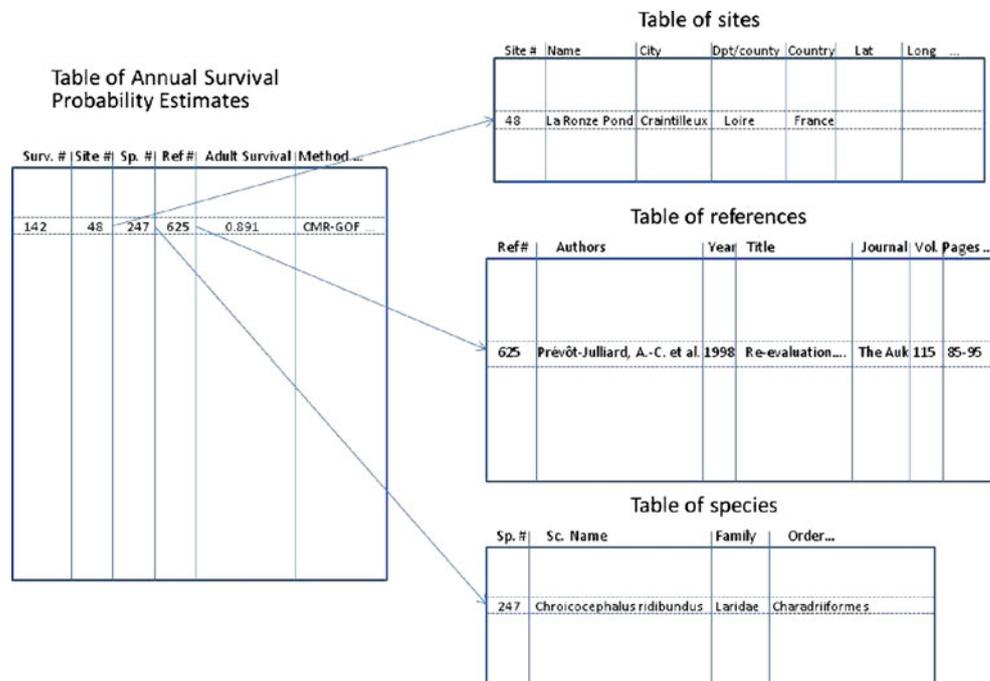
of age and senescence in animals. We present BIDDABA just as an example of a demographic base to address questions of general interest, with no plea to pretending it is better or more relevant than any other one.

In BIDDABA, four different types of demographic parameters were considered and stored in distinct tables: survival probabilities, and, on a more restricted basis, breeding proportions, fecundities and recruitment probabilities. Species were also linked to a table containing estimates of age at first reproduction (AFR) defined at the species level, and of adult body weight, generally obtainable from different sources such as handbooks (e.g., Del Hoyo et al. 1992).

An example of the role of data quality in evolutionary biology: revisiting Bergmann’s rule

Popy et al. (submitted) used BIDDABA to revisit Bergmann’s (1847) rule, according to which body mass should increase with latitude/elevation. Among the many mechanisms for such an increase, the heat conservation hypothesis is the most widely accepted. Because of the general positive relationship between body mass and survival (see, e.g., Gaillard et al. 1989), a correlated increase in survival rates with elevation is expected. Popy et al. (submitted), based on mean elevation estimates derived from regional Atlas data from the Alps and Pyrenees, investigate further potential underlying mechanisms. They look in particular to a potentially causal relationship between demography and metabolism, "slow" life-history strategies being

Fig. 1 The organization of a demographic database: the sites, species and references are organized as separate tables linked to tables of demographic estimates through relationships. Here, just a table for annual adult survival probability is shown, using the example of the estimate of adult survival in the Black-headed Gull *Chroicocephalus ridibundus* provided by Prévot-Julliard et al. (1998)



expected to be prevalent at high elevations as a consequence of the shortening of the breeding season and harsher conditions.

Based on 73 species, Popy et al. (submitted) thus tested for a direct effect of elevation on species survival rates, using a path analysis (Shipley 2002) and controlling for body mass and phylogenetic relationships, for the latter using independent contrasts. Calculations were made using APE (Paradis et al. 2004), a specific tool in the statistical language R (R Development Core Team 2006), and Pendek version 1.03 (Purvis et al., unpublished). Three path models are compared assuming respectively that (1) elevation influenced survival rates both directly and indirectly through body mass, (2) the effect of elevation on survival rates was only indirect through body mass, and (3) the effects of elevation and body mass were independent (Table 2).

The range of species considered required the use of estimates stemming from a variety of methods, and therefore potentially affected by a variety of biases (Clobert and Lebreton 1991). The increase in survival estimates for the same species over time induced by methodological progress is illustrated and discussed by Clobert and Lebreton (1991) and Prévot-Julliard et al. (1998). Popy et al. (submitted) thus consider an additive effect, the “demographic estimation method”, each method being given a score (1, 2 or 3) reflecting an order of expected quality from low to high (Table 2). For each species, the survival estimates stemming from the methods of highest rank were retained, and when several such estimates were available, the mean value was used.

Results (Table 3) showed that, as predicted by the a priori quality ranking, the estimated survival rates increased with the quality of the survival estimation method, i.e., a priori poor methods tended to underestimate survival. In the preferred model (Table 3), survival increased independently with both body mass and elevation, while bringing no support to Bergmann’s rule (no direct effect of elevation on body mass), for which evidence is known to be difficult to obtain when considering a wide range of non-related species (Blackburn et al. 1999). The direct effect of elevation on survival rates matches the prediction of an adjustment of life-history strategies to the deterioration of

reproductive performance as a result of changes in ecological conditions with increasing elevations.

The first interest of controlling for methodological quality is to remove bias. However, there are two further, less obvious, interests. First, some variation is removed from the residual source of variation and attributed to the additive method quality effect. As a consequence, the power of the tests, or equivalently of model selection, is enhanced, although here, model 3 is still preferred when quality is not considered. Second, the whole data are used for estimating the effect of, say, elevation, the bias of some methods being evaluated and corrected at a reasonable cost, i.e., based on few degrees of freedom, by using an additive effect. Although methods were ranked here a priori, considering in greater detail the methods used in such a database should help evaluating the advantages and disadvantages of various methods in terms of bias and precision.

This example, restricted to a small number of species and to interspecific comparisons, clearly does not close the issue of change in demography with elevation, which could be best based on intraspecific comparisons (see, e.g., Gayon 2000 about intra- and inter-specific allometry). Such approaches could be facilitated by a wider availability of estimates, in particular with method quality control, shown here as fairly straightforward to consider.

An example of the interest of a demographic database for conservation biology

Niel and Lebreton (2005), based on a comparative approach over 13 bird species, considered as being at their maximum growth rate per year λ_{\max} , investigated empirically the invariance of λ_{\max}^T , the maximum population growth rate using generation time T as the time unit. The value of this “Maximum growth rate per generation” is close to 3 among birds. Theoretical arguments for its invariance are discussed by Charnov (1993). This invariance implies an inverse relationship between generation time and maximum growth rate per year: $\lambda_{\max} \approx \exp(\frac{1}{T})$ (Niel and Lebreton 2005). As the maximum growth rate per year reflects a general ability of each species to stand man-induced increases in mortality, any estimate of generation time, once converted into an

Table 2 A priori ranking of the survival estimation methods according to their quality (after Popy et al., submitted)

| Quality rank | Method |
|--------------|--|
| 1 | Lack–Farner, return rates, others, no information |
| 2 | Capture–mark–recapture models (single state or multistate), analysis of dead recoveries, Haldane’s method, analysis of telemetry data |
| 3 | Capture–mark–recapture models (single state or multistate) with goodness-of-fit test, analysis of dead recoveries with goodness-of-fit test, analysis of mixture of dead recoveries and capture–mark–recapture |

Table 3 Results of path analysis models for revisiting Bergmann’s rule (after Popy et al., submitted)

| Paths included in the model | | | | Model fit | | | |
|-----------------------------|------------|-------------|-------------|-------------|----------|-------------|--------------|
| ELEV → LBW | LBW → LALE | ELEV → LALE | METH → LALE | Chi-square | df | P level | BIC |
| × | × | × | × | 0.955 | 2 | 0.62 | −7.6 |
| × | × | | × | 4.11 | 3 | 0.25 | −8.7 |
| | × | × | × | 1.36 | 3 | 0.71 | −11.5 |
| | × | × | | 0.41 | 1 | 0.52 | −3.9 |

Preferred (minimal BIC) model in bold

LALE log adult life expectancy, *LBW* log body weight, *ELEV* mean species elevation, *METH* index of statistical estimation method quality, *Chi-square* model fit chi-squared statistic, *df* degrees of freedom, *P level* *P* level of chi-square, *BIC* Bayesian information criterion

estimate of maximum growth rate based on the relationship above, provides thus quite a useful piece of information in relation with the conservation status of species. The life-history strategy of species is not directly considered in the criteria of conservation status by IUCN (Collar 1997), even if it is indirectly present, and briefly mentioned by Collar (1997, p. 19). Desprez (2009) used BIDDABA to produce estimates of generation time at a broad scale and, accounting for phylogenetic relationships, systematically compared them to the conservation status by IUCN (<http://www.iucnredlist.org/search>). She based her analysis on the 119 species in BIDDABA for which demographic information was complete enough to feed a matrix model and which were present in the supertree of birds provided by Davis (2008).

Clearly, the maximum population growth rate, expressed through its correlate, generation time, is strongly linked to conservation status (Fig. 2). Indeed, Desprez (2009) convincingly explores ways of estimating generation time based on partial data, in particular when only an estimate of adult survival is available. She goes on to investigate predictions of the conservation status for the Nazca Booby *Sula granti*, a local form recently upgraded to species level status. While IUCN ranks Nazca Booby as a species “of least concern” because of its large non-fragmented distribution (<http://www.birdlife.org/datazone/species/index.html?action=SpcHTMDetails.asp&sid=30136&m=0>), the demographic approach suggests it is better ranked as “vulnerable”. By using general comparative relationships, Desprez (2009) indeed extends in quite a robust fashion the “surrogate species” approach, according to which information from a closely related taxon/species is used to predict some quantities of interest for a poorly known taxon. It seems clear that explicitly accounting for demography might be of interest to IUCN, in particular because it is a quantitative criterion much more easily estimated than probabilities of extinction or even rates of decline.

Even if a careful look at specific results shows some outliers and incoherence in the data, the relationship in Fig. 2 shows the general coherence of the approach. The systematic use of modeling, and an expert look at outliers,

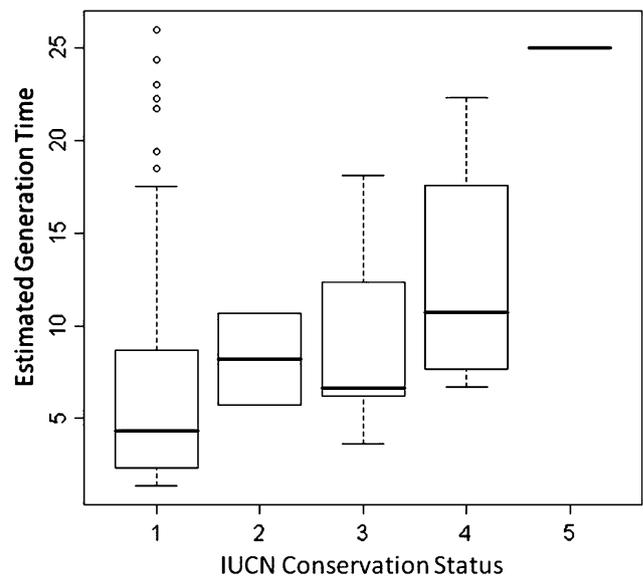


Fig. 2 Relationship between IUCN conservation status (1 least concern, 2 not threatened, 3 vulnerable, 4 endangered, 5 critically endangered) and estimated generation time for 119 bird species (after Desprez 2009, Fig. 4 pro parte)

thus appears as a way of checking coherence in such a database.

What is needed for a larger database?

The first characteristic of a bird or vertebrate database is that it is a small database in terms of number of records (estimates of a particular demographic parameter for a given species in a given site and time interval, from a given literature reference). The number of records will be at most in the thousands and is by no means comparable to that in “large” databases: Genbank currently holds more than 82 million sequences (<http://www.ncbi.nlm.nih.gov/Genbank/>)!

The relationships between tables are also moderately complex, even if those in Fig. 1 are but a part of the whole set of relationships; requests for specific biological

questions can thus be addressed in a fairly straightforward fashion. The development of user-friendly tools for searching and retrieving data seems within easy reach. Links to external taxonomic lists, and to phylogenetic information, as well to GIS, and literature databases should also be fairly straightforward. Given the constant progress in the quality and availability of such information, a great flexibility must be preserved in the possibilities of establishing these links. Our current experience with quality assessment indicates development in this direction will be both useful and straightforward (type of model used, software, lack-of-fit or overdispersion coefficient estimate, sample size, length of time series, etc.).

The main complexity clearly lies in the definition of fields, in a fashion flexible enough to cover the way demographic flows are addressed in current empirical population research. Concerning survival, for instance, “immature survival” can be represented in a variety of fashions:

- as a first-year survival probability (from spring to spring), after which adult survival may apply;
- as a first calendar year survival probability (from spring to December 31), after which adult survival may apply;
- as an overall survival probability from spring of birth to age at first reproduction;
- in each case, either from fledging, or average age at ringing (common for precocial chicks), etc.

Another example concerns first-year “apparent” survival which may combine genuine survival (estimable in principle from dead recovery analyses) with fidelity to the study area (see, e.g., Cooke and Francis 1993). In general, live recapture analyses will only provide an estimate of the product of survival probability by a fidelity probability, which will be, as a consequence, highly sensitive to the scale of the study that must thus be carefully described for a proper interpretation of estimates.

Similar difficulties exist for probabilities of breeding, notably with the large biennially albatrosses *Diomedea* spp. (Weimerskirch et al. 1997), and indeed for all kinds of parameters. The description of the environment in the study site, notably in the presence of a frequent bias towards favorable sites for the species under study, requires specific reflections.

In a general fashion, the potential complexity of the fields and data, and the communication with existing databases, implies that careful and structured descriptions of the data stored are unavoidable. This point is among those discussed in the next section.

In a parallel fashion, quality control, here briefly illustrated concerning statistical methods, has to be extended to encompass sample sizes, heterogeneity in data and sampling, environmental covariates considered, etc.

Tools for depositing data have then to be developed, as analogues of “Sekin” and “Bankit” in Genbank (<http://www.ncbi.nlm.nih.gov/Genbank/>). Tools for updating or revising data already in the database are also needed. In our limited experience, implementing data in a retrospective fashion based on published articles is extremely time-consuming, and often inefficient: a key role for such a database is to collect information more detailed and usable in a more straightforward fashion than that in published papers. Such a database could also hold original datasets (such as capture histories or in the form of statistics sufficient for a wide class of models) to make them widely available for further analyses.

The outline of an international project

On these premises, how can one foresee the development of a large-scale bird demographic database, later expandable as a vertebrate demography database? The database structure and maintenance must be professional and open enough to make it user-friendly and attractive. This is why it can only be conceived as a wide international project for developing a database publicly accessible on the web. The technical development of such a database follows the usual steps: *planning*, *analysis*, *design*, *implementation* and *maintenance*.

The *planning* phase has first to make decisions concerning the connection with existing databases, the availability of data in disconnected databases being hardly a progress compared with the availability in scientific papers (Edwards et al. 2000). Contact should be established with similar existing databases (see “Introduction”) to decide if a common project can be set up, or if some type of interconnection is preferred. While, technically, the size of the databases concerned makes a single integrated project feasible, such a project might appear quite undesirable to groups having already heavily invested in database development. The interconnection is nevertheless costly in terms of metadata, i.e. data descriptions, and conversion procedures required for ensuring a reasonable degree of interconnectivity. Contact with databases with a wider scope, and in first rank with the “Global Biodiversity Information Facility” (GBIF; Edwards et al. 2000) is also a priority. In the long term, if a role analogous to that of Genbank is looked for, support from major ornithological journals is needed to evolve towards recommended or compulsory deposit of demographic estimates prior to publication. A key question is whether such a database concentrates on estimates only, or is widened to consider full datasets. The latter view clearly makes sense in the long run, and would be in line with the current policy of major journals (Whitlock et al. 2010).

The *analysis* phase will benefit from the fairly straightforward relational structure discussed above. A working committee including potential users will be needed to work on the variety of demographic parameters format and definition needed, to benefit from a bottom-up approach. The EURING format (http://www.euring.org/data_and_codes/index.html) for ringing and recovery data is an example of such an effort. These formats and definition will constitute an “ontology” (Guarino 1998), i.e., coherent meta-data detailed and structured enough for providing unambiguous descriptions of the types of data in the database. The discussion of terminology by Thomson et al. (2009) is a first step towards such an ontology. For entering, updating and extracting data, a similar (or the same) committee will have to prepare a list of functions, technically translated into a function-to-data matrix. At this stage, the people needed (analysts, database and data administrators, network administrators, technical writers, etc.) must be identified.

The logical and physical *design* will be better based on a prototype database, resulting from a thorough evolution of an existing database such as BIDDABA. Given the size and type of relationships, Microsoft Access is probably a convenient tool for a first *implementation* of a public vertebrate demographic database, but as much independence as possible from specific hardware and software is recommended (Borer et al. 2009), in particular for long-term *maintenance*. In this respect, it is noticeable that Genbank works with text files.

The accessibility, maintenance and visibility of such a database require that it is run by an operator who can follow through the turnover of people and changes in computer systems, and bring in and/or encourage as many partnerships as possible. EURING, even if in principle only European, seems a structure with potential for hosting such a project.

Given the level of coordination and cooperation looked for, a scientific committee will be needed. A project leader is needed to follow the system development life cycle, coordinate the research of funding, and manage contacts.

The first steps might be:

- (a) look for Initial funding: 2010;
- (b) first technical meeting: early 2011;
- (c) improve prototype database and seek major funding: 2011.

The support of The EURING conference scientific community to such a project would be invaluable, and we hope we have convinced you of its interest.

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