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HOW DO SPECIES' CHARACTERISTICS INFLUENCE THE COST OF INBREEDING?

Systematic Review Protocol

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1.   Background

The genetic diversity contained within threatened or endangered species is relevant to their conservation in a number of ways. First, many populations of these species are isolated and consist of small numbers of individuals. Such populations may have little genetic variation, and this could hamper their ability to adapt to changing or future environmental conditions through natural selection, reducing their potential to persist. A more pressing concern is that these small or isolated populations often consist of closely related individuals, and mating among these close relatives can lead to inbred offspring that suffer immediate health problems. This can act as an additional burden on the populations of endangered species, exacerbating other problems caused by lack of suitable habitat, exploitation and environmental change. Finally, similar problems can occur due to inter-mating between isolated and ecologically divergent populations. This may occur if human-aided movement of species brings previously separated populations into contact.

The study of these genetic risks and threats as applied to the conservation of wild species has become known as conservation genetics. Our aim here is to undertake a systematic synthesis and appraisal of one aspect of the large and growing literature on conservation genetics. This will enable us to understand whether we can draw general conclusions regarding the importance of genetic diversity to the sustainability of wild populations, and will assist in the integration of genetics knowledge and concepts into conservation. In particular we wish to understand where, and in which species, genetic problems are most likely to develop, with a view to establishing an objective and generic framework to better advise those responsible for species conservation.

This review deals with the impacts of inbreeding on fitness, and the threats to population persistence that this might incur. Inbreeding depression is a cost in fitness suffered by offspring of mating that has occurred among related individuals. This cost to fitness is caused when recessive genes that confer a detrimental phenotype are expressed in the homozygous state, or when benefits to fitness through heterosis are obviated (Keller and Waller, 2002, Hedrick and Kalinowski, 2000). Populations that are isolated in the landscape may be at particular risk of suffering adversely through inbreeding effects. This is because when such populations are small, or suffer a reduction in size, mating among relatives becomes more likely, and any genetic variation that is lost through drift cannot be replenished through migration. In other words the populations of greatest concern are thought to be those that are isolated from migration and have a low effective size.

It is important to note that inbreeding (and its associated cost) is a relative rather than an absolute measure (Keller and Waller, 2002). Inbreeding among relatives is always measured relative to a reference population. For example, the cost of inbreeding could be measured by experimentally self-fertilising individual plants and comparing the fitness of the resulting progeny to those derived from random mating within the same study population. The inbreeding coefficient of the inbred cross measures the extent of inbreeding relative to randomly mated individuals, which are defined as the unrelated reference population. Alternatively, one could measure the fitness of offspring within a single inbred population and compare this to the fitness of individuals arising from crosses between this and a separate population. This latter example includes cases of genetic rescue and heterosis where individuals within historically isolated and inbred populations can experience an increase in fitness after individuals from a neighbouring population are introduced.

Although inbreeding effects in natural populations have been reviewed (Hedrick and Kalinowski, 2000, Crnokrak and Roff, 1999, Keller and Waller, 2002), the existing syntheses need updating given the continued growth in the evidence base since these earlier publications. In addition, while one of these reviews is meta-analytic, none are systematic, and thus they may represent a biased view of the available evidence. Given this, there is a need for a new, up-to-date systematic review on this subject area, which can provide an overview of the evidence in order to assist species conservation. Furthermore, the relationship between neutral genetic variation within populations and the cost of inbreeding has not yet been investigated. There is a large body of evidence from molecular markers that documents this genetic variation within populations. It would be useful to know whether these studies contain any information that may be used to understand or predict the potential risks and magnitude of inbreeding effects in either species or their component populations. Therefore, in this systematic review our primary focus will be on the fitness costs of inbreeding in natural populations and the distribution of these effects across species with differing mating systems, life-histories and ecologies. As a secondary question, we will assess the relationship between the cost of inbreeding and levels of neutral variation retained within populations. The rationale for this secondary question is to ascertain whether variation measured with neutral markers captures information on effective population size and the purging of deleterious alleles that is relevant to inbreeding effects. We anticipate that our review has the potential to be useful to conservation, because it links species' attributes that are easy to measure with fitness effects that could influence population persistence.

2.   Objective of the Review

2.1   Primary question

What is the effect of inbreeding on fitness components within populations?

Population   Any natural population
Exposure   Inbred individuals/populations/sub populations
Comparator   Non-inbred individuals/populations/sub populations
Outcome   Difference in fitness

2.2   Secondary question
These secondary questions are of significant interest to the review.

How do a species' characteristics influence the effect of inbreeding on fitness components within populations?

Do levels of genetic variation within populations correlate with the effect of inbreeding on fitness components within populations?

3.   Methods

3.1   Search strategy

3.1.1 Scope of search

We will search the following databases for relevant literature and data:

ISI Web of Science
Scopus
JSTOR

Our experience in reviewing outbreeding effects (Whitlock et al., 2009) has indicated that it is inefficient to search grey literature, particularly theses, as the latter are usually published in the primary literature. Searching the libraries of local NGO organisations during this earlier review also yielded no relevant hits, since the data we are interested in is primarily published in the peer-reviewed literature; therefore we are excluding these searches from the strategy for this review protocol.

Bibliographies of all reviews identified as relevant during assessment of their full text (according to section 3.2, and including those in Table 1) will be searched for further material. Once all relevant literature has been identified and collected, we will contact key research groups publishing on the subject area of our review to determine whether further unpublished data exist that are relevant to the problem.

3.1.2 Search terms

We will use the search terms set out in Appendix A1 to retrieve articles from the databases specified above. The search terms to be used fall into the following categories:

Inbreeding (Exposure) terms	Include commonly used terminology relating to inbreeding
Fitness (Outcome) terms	Include survival, mortality, fitness, heterosis and related terms (inbreeding depression/ cost of inbreeding)

Search terms were identified by reference to articles cited in, and that cited published traditional reviews, and by consultation with the subject experts within the review group. The individual terms or phrases will be combined by OR within category, then for each database, these sets will be combined by AND to yield the final set of results for each database. The results from each database will be combined in an ENDNOTE library in order to create a complete database of putatively relevant articles for this review.

The search may be modified further to adjust specificity and sensitivity in relation to the functionality of the different data sources. Records of the search strategy used will be maintained to ensure repeatability and transparency, and amendments made to the review protocol as necessary.

3.2   Assessment of study relevance

We will assess studies for inclusion in the review based on a hierarchical assessment of relevance by scanning article titles, followed by reading the abstract of articles with relevant titles, followed by reading the full-text of articles with relevant titles and abstracts. Studies will be deemed relevant based on the presence of the desired subject, exposure and comparator (control and inbred mating or crosses within natural populations) and outcome (fitness) measurements. Studies that include information that will allow the genetic diversity covariate to be used to address the secondary question will also be included. These will be marked as relevant to the secondary question, and information on genetic variation will be extracted alongside other relevant information. Decisions will be inclusive when there is doubt as to a study's relevance. Studies that obviously do not deal with whole organism biology (e.g. molecular biology, medical or biochemistry studies) will be excluded.

Articles that are either meeting abstracts or book sections will be assessed for relevance as above, and all reasonable effort will be undertaken to recover original data (or summaries thereof) from the authors where it has not also been published in the primary literature.

Review articles will be retained only if their subject is congruent with the main subject of this systematic review, and/ or are likely to contain relevant data. Other general reviews will be excluded.

Species mating system reports will only be included if there is evidence that appropriate crosses have been carried out and appropriate progeny traits have been measured (e.g. progeny traits that are not parental traits; germination, hatching rate, fitness components of progeny).

Dispersal and philopatry studies can only be included if there is evidence that appropriate crosses (inbred/ non-inbred) have been observed or inferred. Molecular parentage analysis is the only acceptable indirect method for inferring pedigree in the context of this study. All such studies must, in addition, contain measurements of appropriate progeny traits (e.g. germination, hatching rate, fitness components of progeny).

Articles that are errata, commentaries, that contain no empirical data, that are QTL or genetic map studies without inbreeding measurements, that focus on humans will all be excluded.

Repeatability of the article selection process will be determined through the assessment of the same literature database (or subset) by two investigators working independently, via kappa analysis. If there are significant discrepancies in relevance assessment between investigators, these will be discussed and the inclusion criteria amended for clarity if necessary.

3.2.1   Study inclusion criteria

Relevant subject(s):

Relevant subjects include natural populations of wild species, at any location globally, and experimental individuals and progeny derived from these within two generations. We define natural populations as those that have been founded by natural/ spontaneous colonisation. However we also consider naturalised or (re-) introduced populations that persist in the absence of further human intervention. Valid study systems include those where:

- All study population(s) are thought to be natural populations (as defined above)

Or

- The range of studied populations includes natural populations, but some populations may have been augmented or reinforced by assisted migration, recently created *de novo* or by recent re-introduction. In this case, it must be known which populations these are, so that they can be excluded prior to analysis.

And

- All considered populations within a single study are from the same species (no interspecific studies, or studies on hybrid swarms will be considered).

  Studies that describe populations with alternative phraseology such as "provenance", "land-race" or "cultivar" will be retained until it can be ascertained from the article full-text whether they fit the criteria stated above. We will not include studies involving species that are agricultural cultivars or strains, or whose populations are under captive management (e.g. zoo populations). In these studies, the inbreeding response of the same species in a natural setting may have been obscured by a potentially complex combination of founder effects, artificial bottlenecks, deliberate or accidental inbreeding, or stock movement. Genetic variation may also have been influenced by artificial selection, or mixture of breeding lines or cultivars. For each study we will consider the possibility of using a subset of populations, where this subset fits with the guidelines set out in this section. The relevance criteria above exclude, for example, human-maintained inbred lines, lab strains, and artificially selected populations.

Exposure and comparator

The comparator takes the form of observed or experimental non-inbred crosses, among individuals within the study population, or between sub-populations. We refer to these non-inbred crosses as "control" crosses (the comparator). Inbreeding is a relative rather than an absolute measure (Keller and Waller, 2002). The primary point of reference relative to which inbreeding will be measured in this review is the individual study population. Under this definition, the comparator ("non-inbred" control crosses) therefore refers to random mating within the study population. The respective exposure includes observed or experimental "inbred crosses" among relatively more related individuals within the study population(s).

However, we will include studies that provide data allowing inbreeding to be evaluated in sub-populations relative to the total population. In this case, the reference "control" crosses (comparator) are those between sub-populations, while the "inbred" crosses (exposure) arise from random mating within sub-populations. This will allow us to include cases of genetic rescue and heterosis within the review (inbreeding between (sub-) populations), in order to provide important context to the costs of inbreeding occurring purely within (sub-) populations.

The coefficient of inbreeding for the exposure group (inbred crosses) must be known for any candidate study population, since this influences the extent of phenotypic expression of inbreeding depression relative to the comparator group (progeny of non-inbred control crosses). Where available, we will also collect and incorporate information on the coefficient of inbreeding in the comparator group (non-inbred control crosses).
Where individual studies measure inbreeding depression in more than one population, data from each of these will be incorporated into the review.

The exposure and comparator crosses can include:

      i.   Experimental crosses among individuals within or among study populations carried out either *in situ* or by removing individuals to an experimental site, garden or artificial population.

    ii.   Observation of naturally occurring mating or crosses between individuals within or among study (sub-) populations. These can include e.g. observed mating that happens after individuals disperse from a natal social group into a neighbouring social group.

Types of outcome:

Measurement of components of fitness among progeny arising from the observed or experimental crosses in the F1 or later generations. This may include survival or mortality, reproductive effort or success, or early-acting components of viability that are unambiguously traits of the offspring rather than of the parents.

Types of study:

We will consider original research results from studies that document inbreeding depression in populations of wild species, including experimental crosses. The relative levels of inbreeding between exposure and comparator groups should be known from pedigree (e.g. either experimental crosses of known inbreeding coefficient against a background of unrelated crosses, or through a well-resolved marker-based pedigree, or through an observational pedigree).

3.3   Potential effect modifiers and reasons for heterogeneity:

We will investigate the effects of a number of sources of heterogeneity (effect-size modifiers) on the observed estimates of effect size. If sufficient data for meta-analysis is available, these will enter the meta-analysis as fixed effects. The effect modifiers we want to consider are as follows:

      i.   Taxon-specific responses (e.g. insect, plant, mammal)
    ii.   Mating system (e.g. inbreeding/ outbreeding/ mixed)
   iii.   Level of genetic diversity in study populations
   iv.   Level of genetic distance or divergence between exposure and comparator groups (this applies especially to the case of inbreeding between sub-populations)
    v.   Physical distance between exposure and comparator crosses
   vi.   Population size (where possible effective size)
  vii.   Population history (large, small, expanding, contracting)
 viii.   Time in generations through which inbreeding has occurred
   ix.   Life history component/ trait type (e.g. reproductive, morphological, viability/survival, early/late), and relationship to fitness, either direct or indirect
    x.   Coefficient of inbreeding within comparator (inbred) group

xi. Dispersal ability of study taxa (since this could influence the expected costs of inbreeding within sub-populations and the retention of diversity within populations)

We have a particular interest in any correlation between levels of genetic diversity and the costs of inbreeding (this is the secondary question we wish to address with this review). Where possible, we will use a database of studies being accumulated in a separate systematic review on neutral genetic variation to complete the effect-modifier dataset on levels of neutral variation in this review.

3.4 Study quality assessment

Once all relevant full-text articles have been gathered, we will assess the quality of the collected literature by determining, for each article, a weighting score based on the presence or absence of attributes that indicate its quality and suitability for inclusion in the meta-analysis. This score will not be used to control inclusion or exclusion of articles from the review, but to understand any relationship between outcomes (effect sizes) and study quality. The attributes to be investigated are summarised in Table 1, below. For each of these, we will assign points depending on whether or not the desired attributes are present in each study.

Table 1 Attributes used to assess the quality of studies short-listed for inclusion in the systematic review

	Design feature	**Study attribute**
Internal validity of study	Comparator and exposure crosses	Do exposure (inbred) crosses take place contemporaneously with control (control) crosses? Yes: 1 point, 0 points otherwise
		Are the pedigrees underpinning the crosses known (because of experimental manipulation; 2 points), estimated by markers (1 point) or estimated by observation (0 points)
	Scale of evidence for relative level of inbreeding between exposure and comparator groups	Is the coefficient of inbreeding known for both the exposure and comparator crosses? Physical distance used as proxy, no pedigree information on relative inbreeding level (0 points). Inbreeding coefficient known for comparator (1 point). Known for both (2 points)
	Outcome measure	Are the outcome measures components of fitness (survival, fecundity, viability; 1 point), or indirect measures of these (growth rate, body mass, size; 0 points)
	Environment for trait measurements	Are the traits measured in the field (2 points), under experimental conditions that closely approximate field conditions (1 point), or under non-native experimental conditions (0 points)
	Study populations	Random selection of populations, or selection stratified over variability in population location/

		distribution/ size (1 point, 0 points otherwise)
		Cost of inbreeding observed in multiple study populations (1 point), 0 points otherwise
	Selection of individuals for crossing experiments, or selection of natural observed crosses	Random selection from a population of possible crosses, or selection stratified over variability in location or timing of crosses (1 point), 0 points otherwise
External validity of study	Observation window for progeny individuals	Fitness consequences of inbreeding within progeny tracked until at least the F_2 generation 1 point, 0 points otherwise
	Status of populations studied	Does the study include re-introduced, or naturalized population(s)? 1 point if all populations were naturally founded, 0 points otherwise

3.5   Data extraction strategy

Data on study characteristics, outcome measures and effect modifiers will be extracted into an excel spreadsheet from in-line text, tables and graphs (the latter using image analysis software, e.g. IMAGEJ or DATATHIEF). Authors will be approached by email where papers present incomplete information on inbreeding effects (e.g. detail on the number of experimental families or on family-level standard deviation is missing).

3.6   Data synthesis and presentation

3.7.1 Effect size metrics

We will employ Hedge's *d* (standardised mean difference corrected for small sample size bias) as our effect size measure. This will be computed using trait values of progeny arising from the control and inbred crosses or mating category. Specifically, we will use family-level trait mean values as the raw data underpinning the effect size summary metric for each study. Thus for the control crosses there will be a mean, μ_C, and standard deviation, σ_C from n_C family-level trait mean values. μ_I, σ_I, and n_I will be derived in the same way from family-level trait mean values for the inbred progeny group. We will calculate the effect size for each study from the raw data provided in data tables, or by approaching the authors for raw data where this is not readily available in published form. Trait values will be transformed to induce approximate normality of distribution prior to computation of effect sizes. This approach involving Hedge's d is hereafter referred to as *scenario 1*.

Our previous experience reviewing outbreeding depression has indicated that estimates of σ and *n* are rarely provided in data tables or graphs. If we are unable to access complete data as above from a reasonable sample of studies, then we will carry out a meta-analysis based around the following log response ratio:

$$\ln\left(\frac{\mu_I}{\mu_C}\right)$$

with notation as above. This expression has a specific meaning within the context of inbreeding depression research. It is an estimate of $-Bf$, where B is a regression coefficient describing the decline in fitness with inbreeding, and f is the inbreeding coefficient in the inbred group. In most experimental, and some observational studies f, the relative extent of inbreeding between inbred and control groups, is known. Therefore B may be estimated by fitting f as a fixed effect in meta-analysis.

3.7.2 Model and hypothesis testing: scenario 1, Hedge's d

The effect size estimates will be meta-analysed initially using a weighted linear fixed-effects model implemented via the S-Plus/R-package METAFOR (VIECHTBAUER, 2010). Effect size modifiers (sources of heterogeneity) will be fitted in this model as fixed effects. We will weight meta-analyses by the reciprocal of the study sampling variance. We may also extend this analysis to consider a weighted a mixed-effects meta-analytic model, in which case study identity will be fitted as a random effect (this can be done using functions in the R package MCMCglmm). This analysis will be useful for handling situations where a study contributes results for multiple traits from a single species (or data from multiple populations). Results from different traits/ populations will enter the model under a common random effects label for case study identity.

The meta effect-size and effect size modifier parameters will be extracted from the model. In the case of the simple fixed effects analysis, significance of each of these parameters will be tested via a z-test against the null hypothesis that the true parameter value is equal to 0. The fixed effects of primary interest are those that describe the life-history, mating system and ecology of the study species.

An omnibus test that any of the effect-size modifiers (as a group) have parameter estimates significantly different from 0 will also be carried out (Viechtbauer, 2010).

Presence of residual heterogeneity among effect size estimates will be tested using the standard Q statistic (Hedges and Olkin, 1985)

3.7.3 Model and hypothesis testing: scenario 2, log response ratio effect size

Under scenario 2 (response ratio analysis) the analysis will follow the structure presented under scenario 1 with the following exceptions:

We will weight the meta-analyses using the following expression (Borenstein et al., 2009):

$S^2 \left(1/(n_I\,\mu_I^2) + 1/(n_C\,\mu_C^2)\right)$

μ_I and μ_C are mean phenotypes for the treatment (inbred) and reference (non-inbred control) groups respectively, S^2 is the pooled study standard deviation, and n_I and n_C are sample sizes in the treatment and reference groups.

95% confidence intervals for the cumulative effect size, and effect sizes for effect-modifier sub-groups will be calculated using percentile bootstrap resampling (Adams et al., 1997), using bias corrected methods where necessary. Heterogeneity among fixed-effects categories (sub-

groups) will be assessed using resampling (permutation of studies across the fixed effects model structure).

3.7.4 Model checking and data presentation

Results of the meta-analysis will be presented graphically using standard approaches such as forest plots for the effect- and meta effect-sizes and funnel plots and normal q-q plots as a graphical check for the presence of publication bias.

3.7.5 Sensitivity analysis

We will run sensitivity analyses to determine the effects of study quality on the outcomes of the meta-analysis. This will involve defining two or more groups based on the study quality score (e.g. "high" and "low" study quality), and fitting these groups as categorical fixed effects in the meta-analysis (Section 3.3).

We will run similar sensitivity analyses where we identify studies that contribute individual results that are outliers. In this case the outlier studies(s) will be excluded to investigate the dependence of the results on these extreme values.

Publication bias can result in a "file drawer problem", where negative, non-significant or inconsistent results are never published. We will assess the presence of this publication bias visually using funnel plots of study effect size versus study variance (a function of sample size in each study). Small studies that report small or negative effect sizes are unlikely to be published, and this causes asymmetry in the funnel plot. We will also investigate publication bias using Egger's regression (Egger et al., 1997). The sensitivity of the results to the "file drawer problem" will be quantified by calculating a fail-safe n for any significant meta-effect-size (overall effect size) detected. Specifically, we will quantify the number of non-significant study-level effect sizes necessary to reduce the meta-effect size to significance at $\alpha = 0.05$.

The sensitivity of the results to situations in which individual studies contribute more than one (potentially non-independent) effect size will be investigated by random truncation of such studies to a single effect size and reanalysis of the truncated data set.

3.8   Recognised limitations

The approach adopted in this review has several recognised limitations:

Cases is which inbreeding among sub-populations has been measured present some problems in interpretation. First of all inbreeding can occur within sub-populations as well as between them, and in some studies, the measure of among sub-population inbreeding used may subsume both of these. In addition outbreeding depression may contribute to effects on fitness where sub-populations have adapted differently to their respective environments.

3.9   Knowledge transfer strategy

This review is part of a broader project seeking to integrate genetics concepts and knowledge into conservation. The findings of our review will be incorporated into a decision-making framework that will enable conservation practitioners to make use of our findings. On

completion of the review, we will also produce a summary document written in accessible language that can be used by conservation practitioners. This document and the completed review will be made available on the internet, and distributed amongst organisations collaborating in our knowledge exchange project.

In communicating the systematic review and its summary to practitioners we will endeavour to make clear the potential limits and pitfalls in interpreting the results. This is necessary to avoid over-simplification of the results and extrapolation of the findings to situations in which they are no longer relevant.

4.   Potential Conflicts of Interest and Sources of Support

5.   References

ADAMS, D. C., GUREVITCH, J. & ROSENBERG, M. S. 1997. Resampling tests for meta-analysis of ecological data. *Ecology,* 78**,** 1277–1283.

BORENSTEIN, M., HEDGES, L. V., HIGGINS, J. P. T. & ROTHSTEIN, H. R. 2009. *Introduction to meta-analysis,* Chichester, UK, John Wiley & Sons.

CRNOKRAK, P. & ROFF, D. A. 1999. Inbreeding depression in the wild. *Heredity,* 83**,** 260–270.

EGGER, M., SMITH, G., SCHNEIDER, M. & MINDER, C. 1997. Bias in metaanalysis detected by a simple, graphical test. *British Medical Journal,* 315**,** 629-634.

HEDGES, L. V. & OLKIN, I. 1985. *Statistical methods for meta-analysis,* Orlando, Florida, Academic Press.

HEDRICK, P. W. & KALINOWSKI, S. T. 2000. Inbreeding depression in conservation biology. *Annual Review of Ecology and Systematics,* 31**,** 139–162.

KELLER, L. F. & WALLER, D. M. 2002. Inbreeding effects in wild populations. *Trends in Ecology & Evolution,* 17**,** 230–241.

VIECHTBAUER, W. 2010. Conducting meta-analyses in R with the metafor package. *Journal of Statistical Software,* 36**,** 1–48.

WHITLOCK, R., STEWART, G., PULLIN, A., GOODMAN, S., PIERTNEY, S., BUTLIN, R. K., BURKE, T., BRODIE, J., HIPPERSON, H. & ALLEN, S. 2009. Does translocation of individuals between populations result in net cost to fitness in offspring of mixed populations? Bangor, UK: Collaboration for Environmental Evidence.

Appendix 1. Search terms proposed. See 3.1.2

Inbreeding terms
"Inbreeding depression" OR "in-breeding depression"
"Cost* of inbreeding"
Inbreeding
"Inbreeding coefficient"
(inbred SAME cross*) NOT (("Quantitative trait loc*")OR(QTL*))
(inbred SAME mating) NOT (("Quantitative trait loc*")OR(QTL*))
Selfed SAME out*
Selfing OR "sib mating" OR "sib-mating"
"Self-fertilization" OR "Self fertilization" OR "Self-fertilisation" OR "Self fertilisation"
"Optimal outcrossing" OR "Outcrossing distance"
"Benefit* of dispersal"
"Inbreeding avoidance"
"Cost* of dispersal"
"Natal dispersal"
("Distance-depend?nt fitness") OR ("Distance-depend?nt crossing success") OR ("Distance-depend?nt mating success")
Fitness terms
(Depression SAME inbre*)
(Depression SAME fitness)
Survival AND ((ecol*)OR(popul*)OR(evol*)OR(conservation))
Mortality AND ((ecol*)OR(popul*)OR(evol*)OR(conservation))
Fecundity AND ((ecol*)OR(popul*)OR(evol*)OR(conservation))
Longevity AND ((ecol*)OR(popul*)OR(evol*)OR(conservation))
"Life span" AND ((ecol*)OR(popul*)OR(evol*)OR(conservation))
Fitness AND ((ecol*)OR(popul*)OR(evol*)OR(conservation))
"Reproductive output"
"Reproductive success"
Reproduction AND ((ecol*)OR(popul*)OR(evol*)OR(conservation))
Heterosis