THE COMPARATIVE BIOLOGY
OF PHENOTYPIC VARIABILITY

by
Gilbert Cabana
Biology Department
McGill University
1205 Avenue Docteur Penfield
Montréal, Québec
Canada
H3A 1B1

A thesis submitted to the faculty of Graduate Studies and Research in partial fulfillment of the requirements for the degree of Master of Science.

February 1988

ABSTRACT

The present thesis deals with the study of the phenotypic variability of some morphometric and life history characters. The methodological section deals with some statistical problems associated with the measurement of variability. First, two statistical indexes of variability currently used in the biological literature, the Gini Index (G) and the Coefficient of Variation (CV), are compared. It is shown through the use of hypothetical and real data sets that the two indexes are strongly correlated and therefore represent redundant measures of variability. It is then argued that CV should be used instead of G in the comparative study of variability. Secondly, the problem of the scaling of variability, that is the statistical removal of the effect of the mean on univariate statistics of variation such as the standard deviation, is examined. Three statistical models (least-squares regression, major axis, and reduced major axis) are available to scale one variable to another one. It is shown that of these three alternatives, only least-squares regression has the property that residual values are independent of the scaling variable. Thus, it was concluded that least-squares regression should be used when the goal is to statistically remove the effect of one variable on an another one through analysis of residuals.

The comparative section comprises three empirical studies of the variability of morphometric and life history characters. First, a literature survey suggested that phenotypic variability is related to sexual size dimorphism in organisms as varied as insects, deer, and primates. Further analysis of an extensive data set collected from the ornithological literature showed that males of species highly dimorphic in tail length were more variable for this character than those of species with little or no dimorphism. This same effect was found in females, though to a lesser degree. No such trends were observed in a trait reaching less extreme degrees of sexual dimorphism, wing length. These results suggested that in general traits under sexual selection tend to exhibit high degrees of phenotypic variability.

Next, a literature survey of the phenotypic variability of individual fecundity in herbaceous plants, crustaceans, amphibians, reptiles, birds and mammals showed that: 1- in all these taxonomic groups, with the possible exception of the crustaceans, CV of fecundity was independent of the mean, 2- CV was significantly greater and smaller in plants and birds respectively than in the other groups, and 3- In birds and plants, variability of fecundity depended on the reproductive stage considered. In birds, for example, CV of the number of fledgings per nest was about three times as large as CV of clutch size at laying.

The final study showed that the phenotypic variability of fecundity among herbaceous annual plants is significantly higher than among herbaceous perennials. This result was shown to be linked to differences in the pattern of contribution to total fruit output of the population by individuals having different fecundities. Because there are more frequent among annuals, individuals bearing relatively few fruits generally contributed a greater fraction of the population's output than in the case of the perennials. These results suggested that phenotypic variability might be an important correlate of life history strategies like the annual and perennial habits.

RESUME GENERAL

Cette thèse traite de la variabilité phénotypique de certains caractères morphométriques et démographiques de populations animals et végétales. La section méthodologique traite en particulier de problèmes statistiques associés à la mesure de la variabilité. Premièrement, deux mesures statistiques de la variabilité utilisées en écologie, l'Indice de Gini (G) et le Coefficient de Variation (CV) sont comparées. Il est démontré à l'aide d'exemples hypothétiques et réels que ces deux indices sont fortement reliés entre eux et qu'ils représent donc deux mesures redondantes de la variabilité. De plus, une comparaison des deux indices suggère que G devrait être rejeté au profit du CV.

En second lieu, le problème de la calibration ("scaling") de la variabilité, c'est-à-dire du contrôle statistique des effets dûs à la variation de la moyenne sur des mesures de variation univariées telles l'écart-type, est examiné. Trois modèles statistiques (méthode des moindres carrés, de l'axe majeur, et de l'axe majeur réduit) peuvent en principe être utilisés pour éliminer les effets d'une variable sur une autre. Il est démontré ici que seulement la méthode des moindres carrés possède la propriété d'indépendance des valeurs résiduelles par rapport à la variable indépendante. En conclusion, la méthode des moindres carrés doit être utilisés lorsque le but de l'analyse des résiduelles est de contrôler statistiquement les effets d'une variable sur une autre.

La section comparative comprend trois études empiriques de la variabilité de certains caractères morphométriques et démographiques. Premièrement, quelques études publiées de la variabilité des caractères sexuels secondaires sont passées en revue. Une analyse de données tirées de la littérature ornithologique (279 espèces) a démontré que les mâles appartenant à des espèces très sexuellement dimorphiques pour la longueur de la queue sont plus variables que chez les espèces peu ou non

dimorphiques. Un résultat similaire, bien que moins marqué, fut noté chez les femelles. Aucune différence de variabilité morphométrique ne fut observée pour la longueur des ailes, un caractère beaucoup moins dimorphique en général. Ces résultats suggèrent que les caractères soumis à la sélection sexuelle sont en général plus variables que les autres.

Deuxièment, une étude comparative de la variabilité phénotypique de la fécondité chez les plantes herbacées, les crustacés, les amphibiens, les reptiles, les oiseaux, et les mammifères a démontré que: 1- Dans tous ces groupes, sauf posssiblement dans le cas des crustacés, le CV de la fécondité était indépendant de la fécondité moyenne de chaque espèce. 2- Le CV était respectivement plus fort et plus faible chez les plantes et les oiseaux que dans les autres groupes. 3- Chez les oiseaux et les plantes, la variabilité de la fécondité dépendait du stade reproducteur considéré. Par exemple, chez les oiseaux, le CV du nombre d'oisillons laissant le nid était trois fois plus fort que le CV du nombre d'oeufs pondus initiallement.

L'étude finale a démontré que la variabilité de la fécondité (nombre de fruits par individu) chez les plantes herbacées annuelles est plus forte que chez les plantes herbacées vivaces. Ce résultat est lié à des différences dans les patrons de contribution à la production de fruits totale de la population par des individus ayant un nombre différent de fruits. En raison de leur plus grand nombre relatif chez les annuelles, les individus ayant seulement quelques fruits contribuent généralement plus fortement à la production totale que chez les vivaces. Ces résultats suggèrent que la variabilité phénotypique est un facteur important à considérer dans l'étude des stratégies démographiques évolutives.

TABLE OF CONTENTS

Page

TITLE PAGE i

GENERAL ABSTRACT ii

RESUME GENERAL iv

TABLE OF CONTENTS vi

LIST OF FIGURES viii

LIST OF TABLES xi

PREFACE xiii

ACKNOWLEDGEMENTS xiv

GENERAL INTRODUCTION xv

Literature cited xx

CHAPTER 1

A motion for the retirement of the Gini Coefficient from population biology 1

Literature cited 7

CHAPTER 2

On the misuse of functional regression in residual analysis . 11

Literature cited 15

CHAPTER 3

Sexual size dimorphism and phenotypic variability 19
Literature cited 37

CHAPTER 4

The phenotypic variability of fecundity 73
Literature cited 87

CHAPTER 5

The phenotypic variability of fecundity
in annual and perennial plants 126
Literature cited 137

CONCLUSION 146

LIST OF FIGURES

Page

Chapter 1

Figure 1. Relationship between G and CV for plant dry weight in experimental populations of *Trifolium incarnatum* and *Lolium multiflorum* 10

Figure 2. Relationship between G and CV for number of fruits per plant in natural populations of herbaceous plants 10

Chapter 2

Figure 1. a) Relationship between residuals from reduced major axis regression of weaning age on female body weight and female body weight in 63 mammalian species 18

b) Relationship between residuals from least-squares regression of weaning age on female body weight and female body weight . 18

Figure 1. Relationship between sexual difference in mean CV (%) and mean sexual size dimorphism in skeletal measurements of primates 53

Figure 2. Double logarithmic relationship between male and female mean values in birds for:
(a) tail length , (b) wing length 55

Figure 3. Relationship between tail length sexual dimorphism and wing length sexual dimorphism in birds 58

Figure 4. Relationship between log S.D. and log mean for:
(a) male tail length, (b) female tail length
(c) male wing lenth, (d) female wing length 60

Figure 5. Relationship between the index of phenotypic variability and the index of sexual size dimorphism for:
(a) male tail length, (b) female tail length
(c) male wing length, (d) female wing length 65

Figure 6. Frequency distribution for male tail length CV and male wing length CV 70

Figure 7. Two possible types of frequency distribution with same mean and CV 72

Chapter 4

Figure 1. Bivariate relationship between log S.D. and log mean fecundity in various organisms:
(a) Herbaceous plants (fruit number) 115
(b) Crustaceans (brood size) 116
(c) Amphibians (clutch size) 117
(d) Reptiles (clutch size) 118
(e) Birds (clutch size, solid circles),
and mammals (litter size, open circles) 119

Figure 2. Predicted relationships between log S.D. and log mean fecundity in plants, crustaceans, amphibians, reptiles, birds, and mammals 121

Figure 3. Frequency distributions of CV of fecundity in:
(a) plants, (b) crustaceans 123
(c) reptiles, (d) amphibians 124
(e) mammals, (f) birds 125

Chapter 5

Figure 1. Frequency distribution of the CV of fruit number in natural populations of herbaceous annuals (white bars) and perennials (black bars). 141

Figure 2. Frequency distribution of Skewness of fruit number in natural populations of herbaceous annuals (white bars) and perennials (black bars) 143

Figure 3. Relative contribution to the whole population fruit pool by classes of individuals with different fecundities in annuals and perennials 145

LIST OF TABLES

Page

Chapter 1

Table 1. Relationship between G and CV for some families of frequency distributions with n = 3 8

Chapter 3

Table 1. CVs for sexually dimorphic characters and body size measurements in 15 species of horned beetles, Earwig (*Forficula auricularia*), and the Irish Elk (*Megaloceros giganteus*) 42

Table 2. (a) Regression analysis of the scaling of sexual size dimorphism for tail and wing length in birds 45

(b) Regression analysis of the phenotypic variability of tail and wing length for both sexes 45

Table 3. Comparison of phenotypic variability index between species with high sexual size dimorphism ("high group") and species with little or no dimorphism ("low group") for the four trait/sex combinations 47

Table 4. Sexual differences in CV for tail and wing lengths in highly dimorphic species ("high group") and species with little or no sexual dimorphism ("low group") 49

Table 5. Difference in CV between tail and wing lengths for each sex. 51

Chapter 4

Table 1. Phenotypic variability of fecundity in plants, crustaceans, amphibians, reptiles, birds, and mammals 95

Table 2. Regression analysis of the scaling of variability in plants, crustaceans, amphibians, reptiles, birds, and mammals . 107

Table 3. Univariate statistics for CV of fecundity in plants, crustaceans, amphibians, reptiles, birds, and mammal . . . 108

Table 4. Variability in successive avian reproductive characters (clutch size and number fledged) 109

Table 5. Variability in various successive reproductive characters in plants 112

Chapter 5

Table 1. Univariate statistics for mean fruit number per plant, CV of fruit number per plant, and skewness of fruit number per plant in herbaceous annuals and perennials 139

PREFACE

Remarks on style and authorship

As required by the Guidelines Concerning Thesis Preparation, the following article is quoted:

> "The candidate has the option, subject to the approval of the Department, of including as part of the thesis the text of an original paper, or papers, suitable for submission to learned journals for publication. In this case the thesis must still conform to all other requirements explained in Guidelines Concerning Thesis Preparation. Additional material (experimental and design data as well as descriptions of equipment) must be provided in sufficient detail to allow a clear and precise judgment to be made of the importance and originality of the research reported. Abstract, full introduction and conclusion must be included, and where more than one manuscript appears, connecting texts and common abstracts, introduction and conclusions are required. A mere collection of manuscripts is not acceptable; nor can reprints of published papers be accepted.
>
> While the inclusion of manuscripts co-authored by the Candidate and others is not prohibited by McGill, the Candidate is warned to make an explicit statement on who contributed to such work and to what extent, and Supervisors and others will have to bear witness to the accuracy of such claims before the Oral Committe. It should also be noted that the task of the External Examiner is made much more difficult in such cases, and that it is in the Candidate's interest to make authorship responsibilities perfectly clear."

Each chapter of this thesis is based on the text of manuscripts which have been submitted to learned journals for publication. Due to this format, a certain amount of redundancy is inevitable and I apologize to the reader. Chapters 2, 3, 4, are co-authored with Austin Burt and Dr.

Yves Prairie (chapter 2), and Dr. Graham Bell (chapters 3 and 4). For this reason, the pronoun "we" is used instead of "I" throughout these chapters. In all these chapters, I am first author and responsible for data collection, analysis, and entire preparation of first drafts. Chapter 2 is the result of a collaboration with Austin Burt and Dr. Yves Prairie who have commented on early drafts, helped to clarify my arguments and style, and suggested further references. My supervisor, Dr. Graham Bell, helped to write final versions of chapters 3, 4, and 5 in correcting my English, improving the style and organization, and suggesting further analysis of the data.

Acknowledgements

My supervisor, Graham Bell, was invaluable in suggesting ways to correct the style and logic of the manuscripts and providing financial support.

I would also like to thank Austin Burt, Carlos Duarte, Luc-Alain Giraldeau, Vasso Koufopanou, Martin Lechowicz, Timothy Mouseau, and Derek Roff for commenting on early versions of some chapters.

My thanks also go to Ron Kara for preparing the majority of the figures and for being such a proficient table hockey player.

Louis Lefebvre kindly provided access to his personal computer. Merci aussi pour une bouffée d'air frais !

Lastly, my warmest thanks go to my parents, Marcel and Micheline, for their love and support. Cette thèse vous est dédiés.

GENERAL INTRODUCTION

The present thesis deals with the study of the phenotypic variability of biological characters in natural populations. Before introducing the topic of each chapter, I will first define the scope of the study and present some information on the approach that was favoured.

The concept of variation among individuals in a population is fundamental to most fields of population biology, including population genetics, physiological and behavioural ecology, life history studies, quantitative morphology, population management, etc. Variability within populations in morphological, physiological, life history , and behavioural traits, is ubiquitous in nature. Yet, despite this pervasiveness, few empirical generalizations about the phenotypic variability or plasticity of morphometric and life history traits have emerged. Rather, we have a number of theories or models (largely untested) and scattered facts (see reviews by Bradshaw 1965; Grant and Price 1981; Caswell 1983; Schlichting 1986). As pointed out by Grant and Price (1981), empirical studies of variation lag far behind theory. We have a great number of models explaining why and how a certain character should be more or less variable than an other; however, few empirical rules of variability exist. Yablokov's (1974) large compilation and analysis of estimates of variability in mammalian morphometric traits stands as an exception. While a large amount of quantitative information on the variability of morphometric and life history characters published in the form of range or standard deviation is available, data-oriented reviews of phenotypic variability are lacking. It is hoped that the present thesis will help to fill this gap.

Different levels of comparison of phenotypic variability can be distinguished. For a given species, one can examine the variability of different characters, or, alternatively, variability in a particular trait can also be compared among species, or higher taxonomic groups. These two aspects will be treated here, with an emphasis on taxonomic comparisons. This thesis consists of two section. First, a methodological section, which includes two chapters (Chapters 1 and 2), deals with the measurement and statistical analysis of phenotypic variability. In the second part, there follows three chapters on the comparative study of the phenotypic variability of morphometric and life history characters. In Chapter 3, the phenotypic variability of sexually dimorphic morphometric characters is reviewed. The analysis of an extensive data set collected from the ornithological literature on the variability of tail and wing length in species with different degree of sexual size dimorphism is also presented. Chapters 4 and 5 deal with the phenotypic variability of fecundity in natural populations of plants and animals. First, the distribution of phenotypic variability of fecundity between as well as within taxonomic groups such as plants, crustacea, amphibians, reptiles, birds, and mammals is reviewed (Chapter 4). Then, the relationship between phenotypic variability in fecundity and life history is investigated in annual and perennial herbaceous plants (Chapter 5).

Methodological Section

This section includes two statistical notes concerned with the methodology of the quantitative study of variability.

An important problem in the scientific study of variability is certainly how to measure it. Many statistical indices of dispersion have been proposed, including the range, the quartile deviation (Sokal and Rohlf 1981), the Gini coefficient, and the coefficient of variation (CV). A complete review of the advantages and disadvantages of all major indices of dispersion is outside the scope of the present thesis. However, the recent resurgence of the Gini coefficient as a measure of dispersion in plant biology (Weiner and Solbrig 1984; Waller 1985; Weiner 1985) prompted me to compare this index of variation, originally used in economics (Sen 1973), to the coefficient of variation, a measure of variation traditionally used in biology. In Chapter 1, I examine the relationship between the two indexes and discuss their relative merits.

CV (standard deviation / mean) is a measure of relative variation in the sense that it allows comparison of the variability among distributions with different mean values (Van Valen 1980). Underlying its use is the assumption that the standard deviation is positively correlated with the mean. For example, if the standard deviation is independent of the mean, CV will be negatively related to the mean, an undesirable situation since differences in variability, measured by the CV, will be confused with simple differences in mean value among species. Before calculating CVs of different species for a particular character, one should therefore study the relationship between the standard deviation and the mean. To achieve this goal, the following model was fitted by least-squares regression method:

$$\log_{10} \text{S.D.} = a \log_{10} \text{Mean} + \log_{10} b \qquad (1)$$

The relationship between CV and the mean can be obtained simply by substracting $\log_{10}$ Mean from both sides of equation (1):

$$\log_{10} \text{CV} = (a-1) \log_{10} \text{Mean} + \log_{10} b \qquad (2)$$

If $\underline{a} = 1$, the slope of the relationship between CV and the mean for a particular set of S.D. and mean pairs is zero, and variation in CV is independent of the mean. In the cases where $\underline{a}$ departs from the value of one, CV will either increase (if $\underline{a} > 1$), or decrease (if $\underline{a} < 1$) with the mean. With this technique, which will be used throughout the present thesis , it is therefore possible to investigate how relative variability, measured as the CV, scales to the mean. For any value of $\underline{a}$, that is, in all cases irrespective of whether CV is independent or not of the mean, the residual deviations from relationship (1) will constitute scaled indices of variability which can be used to compare the variability in species with different means. Several statistical models (e.g. least-squares, major axis, reduced major axis [Ricker 1973; Harvey and Mace 1982; Seim and Saether 1983]) are available to fit bivariate relationships such as equation (1), and the estimated value of the slope $\underline{a}$ may differ substantially depending on which method is followed. The question therefore arises: Which statistical model to use in the scaling of variability? In Chapter 2, it is shown that only residuals from least-squares regression are independent of the X-variable, the mean in the case of relationship (1). Residuals obtained from other fitting techniques will covary to some degree with the X-variable. Thus, only residuals from least-squares regression estimates of relationship (1) constitute scaled indices of variability, in the sense that they are independent of variation in mean value among species. For this reason, least-squares regression methods will be used in the present thesis to statistically remove the potential effect of the mean on estimates of variability.

Comparative section:

A comparative study of phenotypic variability in some morphometric and life history characters.

Models derived from the theory and results of artificial breeding experiments have played an important role in the study of variation within populations (see review by Grant and Price 1981). Thus, for a particular character, the level of variation found in a population is viewed as the result of the action of factors including immigration, mutation, genetic drift, and selection. While all of these factors may be important in determining the level of variation present in a population, the effet of selection on variation has received a large share of the attention, most probably because the idea of variation, and its elimination (stabilizing selection) or maintenance (disruptive selection) is intimately associated with it. It is therefore tempting to examine the variability of traits that are likely to be under different selection regimes. Sexual selection is generally the accepted explanation for the occurence of highly developed secondary sexual characters in the males of certain species, like in the classical case of the Peacock. In Chapter 3, we first summarize some scattered evidence suggesting that such traits are also in general very variable. We then further test this hypothesis of a relationship between sexual dimorphism and phenotypic variability using an extensive data set culled from the ornithological literature.

No evolutionary change can occur in the absence of genetic variance in fitness. While extensive theoretical work dealing mathematical analysis of selection intensity in terms of fitness variance has been done (e.g. Wade and Arnold 1980), no large scale empirical study of the variability of fitness traits in natural populations has been so far published. In Chapter 4, we present a literature survey of the variability of fecundity of herbaceous plants (fruit number), crustaceans, amphibians, reptiles, birds (clutch or brood size), and mammals (litter size). Three main questions will be examined. First, is CV independent of the mean in each of these taxonomic groups, i.e. do we need to correct for differences in mean values when comparing CVs of species with different mean fecundities ? Next, Are there any differences in phenotypic variability among these same taxonomic groups, and to what extent does variability itself vary within groups? And lastly, Is there any change in phenotypic variability among successive reproductive stages, for example, between clutch size at laying and the number of young fledged in birds ?

Finally, we examine in Chapter 5 the phenotypic variability of fecundity as a correlate of life history. Using literature and original data, we test two opposite hypotheses relating the variability of fruit number per individual plant to life habit (annual *vs* perennial).

LITERATURE CITED

Bradshaw, A.D. 1965. Evolutionary significance of phenotypic plasticity in plants. Adv. Genet. 13: 115-155.

Caswell, H. 1983. Phenotypic plasticity in life-history traits: Demographic and evolutionary consequences. Amer. Zool. 23: 35-46.

Grant, P.R., and Price, T.D. 1981. Population variation in continuously varying traits as an ecological problem. Amer. Zool. 21: 795-811.

Harvey, P.H., and Mace, G.M. 1982. Comparisons between taxa and adaptive trends: Problems of methodology. Pages 343-361. In "Current problems in sociobiology". King's College Sociobiology Group (eds.). Cambridge University Press, Cambridge.

Ricker, W.E. 1973. Linear regressions in fishery research. J. Fish. Res. Board Can. 30: 409-434.

Schlichting, C.D. 1986. The evolution of phenotypic plasticity in plants. Ann. Rev. Ecol. Syst. 17: 667-693.

Seim, E., and Saether, B.E. 1983. On rethinking allometry: Which regression model to use? J. Theor. Biol. 104: 161-168.

Sen. A. 1973. On economic inequality. Clarendon, Oxford.

Van Valen, L. 1980. The statistics of variation. Evol. Theo. 4: 33-43.

Wade, M.J., and Arnold, S.J. 1980. The intensity of sexual selection in relation to male behavior, female choice , and sperm precedence. Anim. Behav. 38: 446-461.

Waller, D.M. 1985. The genesis of size hierarchies in seedling populations of *Impatiens capensis* Meerb. New Phytol. 100: 243-260.

Weiner, J. 1985. Size hierachies in experimental populations of annual plants. Ecology 66: 753-752.

Weiner, J., and Solbrig, O.T. 1984. The meaning and measurement of size hierarchies in plant populations. Oecologia 61: 334-336.

Yablokov. A.V. 1974. Variability in mammals. Amerind, New Delhi.

CHAPTER 1

A MOTION FOR THE RETIREMENT OF THE GINI COEFFICIENT FROM POPULATION BIOLOGY

SUMMARY

The Gini Coefficient (G) has been proposed as a measure of the degree of size hierarchy present in plant populations (Weiner and Solbrig 1984). Another index of inequality or variability is the Coefficient of Variation (CV). The relationship between these two indexes was investigated . It was shown through the use of hypothetical examples and real data sets that the two indexes are strongly correlated. In two data sets, variation in CV explained respectively 86.5 % and 92.2 % of the variation in G. G and CV are therefore two redundant measures of variability. The relative merits of the two indexes were discussed and it was concluded that in future research the use of G should be dropped and CV be used instead.

INTRODUCTION

Weiner and Solbrig (1984) have reviewed and criticized the various uses of the concept of "size hierarchy" in the plant population biology literature. They noted that this concept has been used to qualify three situations: (1) a large variation in plant size; (2) a distribution with a few large individual plants and many small ones; (3) a disproportionate contribution from a few large plants to the total biomass. They criticized as inappropriate the use of standardized measures of skewness based upon the third moment around the mean (g_1) to measure the degree of hierarchy (i.e. in White and Harper 1970, Turner and Rabinowitz 1983). Their main criticism is that g_1 only reflects the second of the three aspects of a "hierarchy" mentioned above. They point out that the main deficiency of this measure of "hierarchy" is that it is insensitive to the degree of variation in plant size (point 1 above). They presented hypothetical examples to show that (1) distributions with very different degree of variability may have the same g_1 (Fig. 1a-c in their paper), and (2), that, conversely, two symmetric distributions with different degrees of variability as measured by the Coefficient of Variation ($CV=SD/X$) may have have equal g_1 (e.g. $g_1=0$ in their Fig. 2a, b). From these examples, they concluded that a highly skewed distribution is no evidence for a strong degree of hierarchy if the coefficient of variation is very low and therefore the difference between the largest and the smallest individual is small when expressed in relative terms. Both of their hypothetical examples suggest that skewness alone is an inadequate measure of inequality or hierarchy and that it should be replaced by the use of CV. Rather than recommending this, the authors propose to use an index of inequality or hierarchy borrowed from the economics literature, the Gini Coefficient (G), to fill the void left by their rejection of the index of skewness as a measure of inequality. G is equal to one half of the arithmetic average of the absolute values of the relative pairwise differences between all observations (Sen 1973), where x_i and x_j stand respectively for the ith and jth observation, and n is the sample size:

$$G = \frac{\sum_{x=i}^{n} \sum_{x=j}^{n} |x_i - x_j|}{2n^2 X}$$

The Gini Coefficient measures how much a population departs from the case where all individuals have the same value (G=0), i.e. how much variability is present in the population, a task that is also performed by the CV (Sokal and Rohlf 1981). As they point out, G has the desirable characteristic of being independent from the mean , that is, its value does not change if each individual's size is raised in the same proportion. This is also a characteristic of CV (Sokal and Rohlf 1981), and this raises the question whether CV and G are just slightly different statistics measuring the same thing.

Here, I show by using some theoretical and applied examples that, indeed, the Coefficient of Variation measures inequality or variability as well as G does, and that its use has many advantages over that of G. Consequently CV should be used instead of G.

RESULTS AND CONCLUSION

First, I will compare the values of CV and G for different hypothetical distributions (symmetric, and skewed). I investigated the relationship between the two indexes for different distributions of three values (Table 1). With such a small number of values it is easy to calculate exactly the general expression for the two indices for each type of distribution (note that the parametric (n used intead of n-1) values for G and CV are used here). First, consider a symmetric distribution with the three values defined as x, x+e, x+2e (Table 1, case 1). By varying the values of x and e, we can obtain symmetric distributions with different CVs and Gs. The general expression for CV and G for this family of distributions is given in Table 1. While CV and G can change for these different symmetric distributions, the ratio G/CV remains constant for any combination of x and e (except for x=0, in which case both G and CV are undefined) (Table 1). Thus for this family of distributions G and CV are redundant. A similar analysis for the other distributions also showed that, for each family of skewed distributions, the ratio G/CV is constant (cases 2 to 4). These ratios, however, depended on the general shape of the distributions, and it is not clear whether the relatively small range in G/CV observed among the 4 hypothetical cases analyzed here (0.471-0.544) is a robust result or just an artefact of the nature of the hypothetical examples used here. The choice of n=3 relies on mathematical simplicity and I leave the burden of finding a more general proof to the mathematically inclined reader. The generality of my results can be investigated by examining the relationship between G and CV in real data sets with relatively large sample sizes (n>10). Weiner (1985) used the Gini Coefficient in a study of size hierachies in experimental populations of two annual plants and provides estimates of G of plant dry mass for several density and soil treatments. For each of these treatments , I calculated CV from his frequency diagrams. A strong positive relationship between G and CV (Fig. 1) indicated that much information is shared between G and CV, as 86.5 % of the variation in G was explained by variation in CV. A similar result was also found in a study of individual fruit production in the field (n between 77 and 448) for 41 herbaceous plant species (Cabana 1988) where 92.2 % of the variation in G was accounted for by variation in CV (Fig. 2). These two examples therefore confirm our previous theoretical result that G and CV are strongly related to each other.

While it could certainly be argue that both kinds of analysis are equivalent and should be used indiscriminately, I propose that CV should be given preference over G for the following reasons. Variability statistics based on the moments around the mean have the advantage that they have been the object of much theoretical work (e.g. Lande 1977; Van Valen 1980) . On the other hand, the statistical behaviour of G is less well known and its indiscriminate use may lead to some pitfalls. For example, in a study of the development of size hierarchies in seedling populations of *Impatiens capensis*, Waller (1985) showed that final seedling dry <u>weight</u> had larger Gs (mean G = 0.310) than cotyledon <u>area</u> only a few weeks after sowing (mean G = 0.182). The author interpreted this difference in G as the possible result of competitive interactions as well as intrinsic differences in growth rate. It is however known from the literature on CV (Lande 1977) that , from geometric considerations alone, the proportions of the CVs of volume(or weight)/ surface/linear measurements are expected to be approximately 3/2/1/. For this reason, weight CVs are routinely divided by three to make them comparable to CVs of linear measurements (e.g. Soule 1982). If G behaves like CV, one would therefore expect that the proportion of weight G/surface area G should be approximately 3/2 or 1.5, which is not too far from the value of 1.70 (0.310/0.182) found by Waller (1985). Again, I do not present here any complete analytical proof that for any initial distribution, quadratic or cubic transformation of each value will result in a respectively approximate doubling or tripling of G. However in the many simulations that I performed with different distributions, such transformations never failed to increase G. Waller's interpretation of his result is therefore, at the least , questionable, since the increase in G found from the cotyledon area to the final dry weight could well be a simple scaling artefact.

CV also has the advantage that it is easily calculated with pocket calculators or with the help of easily obtainable statistical packages , while calculation of G necessitates the writing of specific programs. Lastly, CV has been traditionally used in several biological fields and the accumulation of data on CV of various characters has permitted the construction and test of several hypotheses dealing with variability (e.g. Yablokov 1974; Soule 1982; Lacey et al 1984). If both CVs and Gs are alternatively reported in the literature, the comparative study of variability would become much tedious. Since I have shown that G and CV are approximately equivalent indexes of variability and cannot find any advantages, but only disadvantages, for the use of G over that of CV, I cannot but move for the retirement of the Gini Coefficient from population biology.

LITERATURE CITED

Cabana, G. 1988. The phenotypic variability of fecundity in annual and perennial plants. MS

Lacey, E.P., Real, L., Antonovics, J. , and D.G. Heckel. 1983. Variance models in the study of life histories. Amer. Nat. 122: 114-131.

Lande, R. 1977. On comparing coefficients of variation. Syst. Zool. 26: 214-217.

Salisbury , E.J. 1942. The Reproductive Capacity of Plants. Bell, London.

Sen, A. 1973. On Economic Inequality. Clarendon, Oxford.

Sokal, R.R., and J.E. Rohlf. 1981. Biometry. (2nd ed.) Freeman, San Fransisco.

Soulé, M.E. 1982. Allomeric variation. I. The theory and some consequences. Amer. Nat. 120: 751-764.

Turner, M.D. and D.R. Rabinowitz. 1983. Factors affecting frequency distributions of plant mass: the absence of dominance and suppression in *Festuca paradoxa* . Ecology 64: 1103-1111.

Van Valen, L. 1980. The statistics of variation. Evol. Theor. 4 : 33-43.

Waller, D.M. 1985. The genesis of size hierarchies in seedling populations of *Impatiens capensis* Meerb. New Phytol. 100: 243-260.

Weiner, J. 1985. Size hierarchies in experimental populations of annual plants. Ecology 66: 743-752.

Weiner, J., and O.T. Solbrig.1984. The meaning and measurement of size hierarchies in plant populations. Oecol. 61: 334-336.

White, J. , and J.L. Harper. 1970. Correlated changes in plant size and number in plant populations. J. Ecol. 58: 467-485.

Yablokov, A.V. 1974. Variability of Mammals. Amerind, New Delhi.

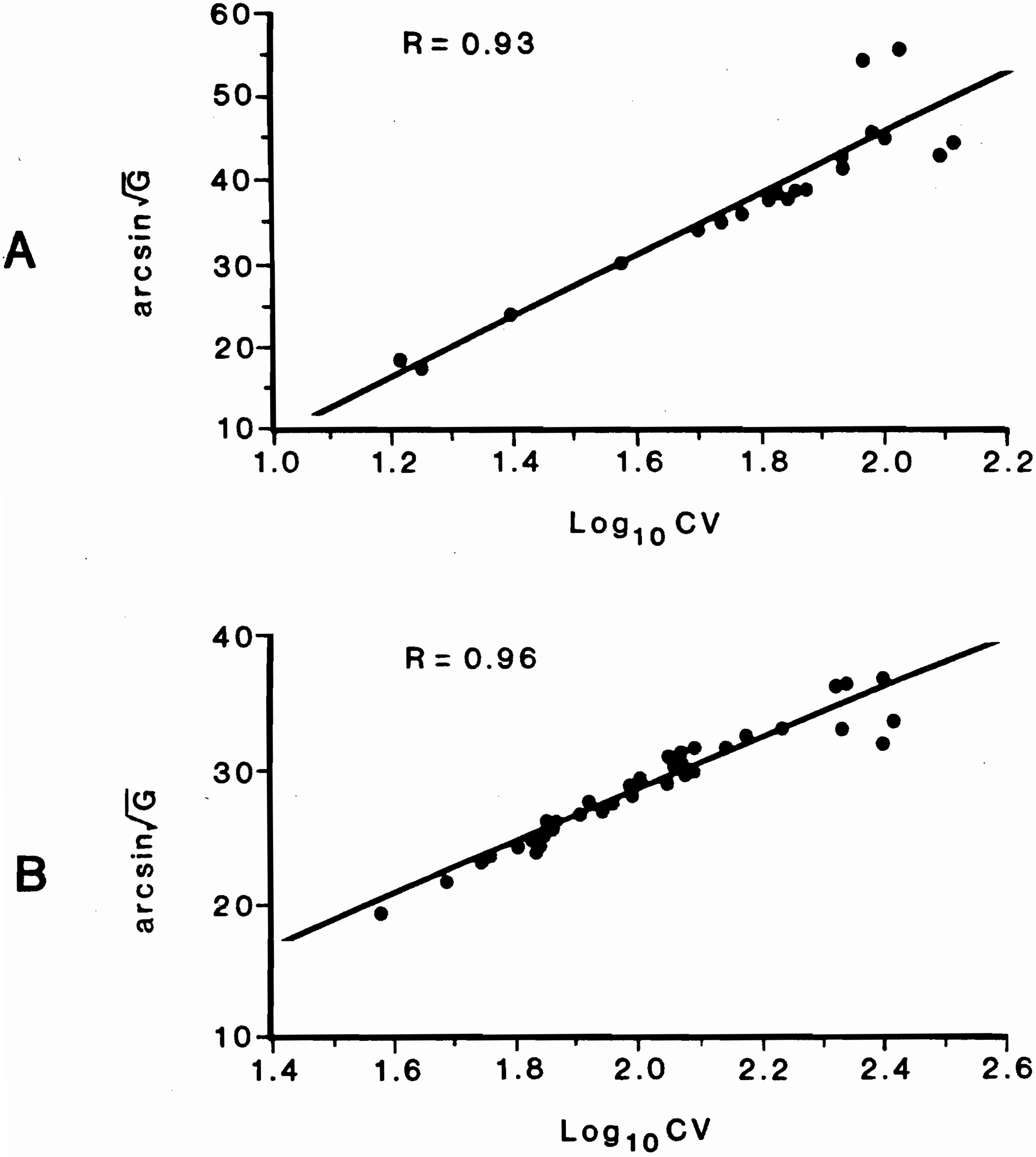
Table 1. Relationship between G and CV for some families of frequency distributions with n=3. Different values of G and CV can be obtained in each family by varying the values of x and e. However, the ratio G/CV is a constant for all possible values of x and e in each family.

DISTRIBUTION	CV	G	G/CV
1. x , x+e, x+2e	$\frac{e(2/3)}{x+e}$	$\frac{4e}{9(x+e)}$	0.544
2. x, x+e, x+6e	$\frac{e(62/3)}{x + 7e/3}$	$\frac{4e}{3(x + 7e/3)}$	0.508
3. x, x+e, x+e	$\frac{e(2/9)}{x + 2e/3}$	$\frac{2e}{9(x + 2e/3)}$	0.471
4. x-e, x-e, x	$\frac{e(2/9)}{x - 2e/3}$	$\frac{2e}{9(x - 2e/3)}$	0.471

Figure 1. Relationship between G and CV for plant dry weight in experimental populations of *Trifolium incarnatum* and *Lolium multiflorum*. Note that angular transformation was applied to G and logarithmic transformation to CV. Data from figures 1, 2, 3, 4, and 6 in Weiner (1985).

Figure 2. Relationship between G and CV for number of fruits per plant in natural populations of herbaceous plants. Transformations as in figure 1. Data from Salisbury (1942) and Cabana (1988).

FIG. 1


A
R = 0.93
arcsin√G
60
50
40
30
20
10
1.0
1.2
1.4
1.6
1.8
2.0
2.2
Log_{10}CV
B
R = 0.96
arcsin√G
40
30
20
10
1.4
1.6
1.8
2.0
2.2
2.4
2.6
Log_{10}CV

CHAPTER 2

ON THE MISUSE OF FUNCTIONAL REGRESSION IN RESIDUAL ANALYSIS

Comparative biology (*sensu* Clutton-Brock and Harvey 1984) differs from experimental biology in that it seeks patterns in observations of unmanipulated or natural systems. It is a method of research which is being used with increasing frequency, for testing hypotheses, describing functional relationships, and deriving predictive relationships. Most work in allometry can be included in this category. Concomitant with the increased activity in comparative biology has come a number of advances in the statistics appropriate for such data, particularily in regression and correlation analysis (Clutton-Brock and Harvey, 1984). Here, we consider two such advances. First, there is the use of residuals from a regression line of one variable (Y) on another (X) to define new, derived variables. This is done in order to remove the efect of X (usually body size) on Y, so that the variation in Y can be examined independently of the variation in X. Taxonomic or ecological differences in the derived variables may then be assessed using analysis of variance, or alternatively, patterns of association among derived variables may be explored using correlation analysis (e.g. Jerison 1973; Cabana et al 1982; Henneman 1983; Swilhart 1984). Second, there is the use of Model II regression methods (Ricker 1973; Sokal and Rohlf 1981) to describe the functional relationship between the two variables (e.g. Martin 1981). Since there is often no biological reason to distinguish betwen dependent and independent variables, the standard least-squares regression model can be inappropriate (but see Wolpoff 1985), and so a functional regression model is applied, usually either major axis regression or reduced major axis regression (Harvey and Mace, 1981;Seim and Saether 1983). In this paper, we are concerned with the mariage of these two methods: the use of residuals from functional regressions to define new scaled variables (e.g. Gittleman and Harvey 1982; Harvey and Clutton-Brock 1985; Gittleman 1986a, b; Worthy and Hickie 1986). We shall demonstrate that such variables are not independent of the X-variable, thus defeating the purpose of using them as scaled variables.

Consider two variables, Y and X, and the two equations relating one to the other:

Least-squares regression : $Y_i = b_s X_i + a_s + e_{si}$ (1)

Functional regression : $Y_i = b_f X_i + a_f + e_{fi}$ (2)

where b_s and b_f are slopes, a_s and a_f, are intercepts, and e_{si} and e_{fi} are residuals. Since functional regression lines pass through the bivariate mean (X,Y) (as do least-squares lines), the intercept of the functional regression is:

$$a_f = \overline{Y} - b_f\overline{X} \qquad (3)$$

If we substitute this expression with equation (2) and rearrange, we get:

$$e_{fi} = Y_i - b_fX_i + b_fX_i - \overline{Y} \qquad (4)$$

We now substitute the least-squares equation of Y_i (equation 1) into this expression and rearrange:

$$e_{fi} = (b_s - b_f)X_i + (a_s + b_fX_i - \overline{Y}) + e_{si} \qquad (5)$$

This expression has the familiar form of a linear regression equation, here describing the relationship between the residuals from the functional regression and the X variable. This relationship has a slope equal to the difference between the the slopes of the original functional and least-squares regressions: $b_s - b_f$. Indeed, this is true of any line passing through the bivariate mean $(\overline{X},\overline{Y})$, and only residuals from the least-squares line are truly independent of the X-variable (see also Gujarati, 1978:45). Since functional regression slopes are steeper than the least-squares slopes, the value $b_s - b_f$ will be negative for positive b_s and positive for negative b_s. Note also that the residuals in our relation (equation 5) are equal to those from the original least-squares regression (equation 1) and the standard error of the slope relating e_{fi} to X is the same as that of the least-squares regression relating Y to X.

To illustrate this point, we have used the data set on life histories of 63 species of carnivores given by Gittleman (1986). Among these species, there is a significant association between weaning age (days) and female body weight (kg) ($r=0.67$, $p<0.001$), which can be described by the equations:

Least-squares regression:

$$\log_{10}(\text{weaning age}) = 0.23*\log_{10}(\text{weight}) + 1.74$$

Reduced major axis regression:

$$\log_{10}(\text{weaning age}) = 0.34*\log_{10}(\text{weight}) + 1.67$$

The residuals from the functional regression are related to female body weight with a slope of 0.23-0.34 = -0.11 (Fig. 1a); this association is statictically significant ($p<0.01$) ands accounts for 16.2 % of the variance in the reduced major axis residuals. In contrast, residuals from the least-squares regression are independent of female body weigth ($r = 0$, $b = 0$, Fig. 1b).

To summarize, residuals from a functional regression are not independent of the X-variable, and thus should not be considered as scaled indices with the effects of that variable removed. Note that this is true whether one is using vertical residuals or residuals perpendicular to the slope of the functional regression, for these will be related to each other in a constant proportion (i.e they will correlate exactly with one another). Thus comparisons of residuals from functional regressions among taxonomic or ecological groups will not be independent of differences in the X-variable (*contra* Gittleman and Harvey 1982; Harvey and Clutton-Brock 1985; Gittleman 1986a, b). Furthermore, since residuals are a function of the X-variable (equation 5), any two such residual variables derived using the same X variables (e.g. body weight) will give spurious positive correlations. Thus correlation matrices of these derived variables (e.g. Harvey and Clutton-Brock 1985; Gittleman 1986) should be interpreted with caution. It is more appropriate to correlate residuals from least-squares regressions; this technique is identical to the use of partial correlations (described in Sokal and Rohlf 1981).

LITERATURE CITED

Cabana, G., Frewin, A., Peters, R.H., and L. Randall. 1982. The effect of sexual size dimorphism on variations in reproductive effort of birds and mammals. Amer. Nat. 120: 17-25.

Clutton-Brock, T.H., and P.H. Harvey. 1984. Comparative approaches to investigating adaptations. p 7-29. In "Behavioural Ecology. An Evolutionary Approach". 2nd ed. Krebs, J.R. and N.B. Davies (eds.). Blackwell Scientific Publications, Oxford.

Gittleman, J.L. 1986a. Carnivore brain size, behavioral ecology, and phylogeny. J. Mammal. 67: 23-36.

Gittleman, J.L. 1986b. Carnivore life history patterns: Allometric, phylogenetic, and ecological associations. Amer. Nat. 127: 744-771.

Gittleman, J.L., and P.H. Harvey. 1982. Carnivore home range, metabolic needs and ecology. Beh. Ecol. Sociobiol. 10: 57-63.

Gujarati, D. 1978. Basic Econometrics. McGraw-Hill, New York.

Harvey, P.H., and T.H. Clutton-Brock. 1985. Life history variation in primates. Evolution 39: 559-581.

Harvey, P.H., and G.M. Mace. 1982. Comparisons betwen taxa and adaptive trends: problems of methodology. pages 343-361. In "Current Problems in Sociobiology". King's College sociobiology group (eds.). Cambridge University Press, Cambridge.

Henneman, W.W. III. 1983. Relationship among body mass, metabolic rate and the intrinsic rate of natural increase in mammals. Oecologia 56: 104-108.

Jerison, H.J. 1973. Evolution of the Brain and Intelligence. Academic Press, New York.

Martin, R.D. 1981. Relative brain size and basal metabolic rate in terrestrial vertebrates. Nature 293: 57-60.

Ricker, W.E. 1973. Linear regressions in fishery research. J. Fish. Res. Brd Can. 30: 409-434.

Seim, E., and B.E. Saether 1983. On rethinking allometry: Which regression model to use? J. Theor. Biol. 104: 161-168.

Swilhart, R.K. 1984. Body size, breeding season length, and life history tactics of lagomorphs. Oikos 43: 282-290.

Wolpoff, M.H. 1985. Tooth-size scaling in a human population. Theory and practice of an allometric analysis. p. 273-318. In "Size and Scaling in

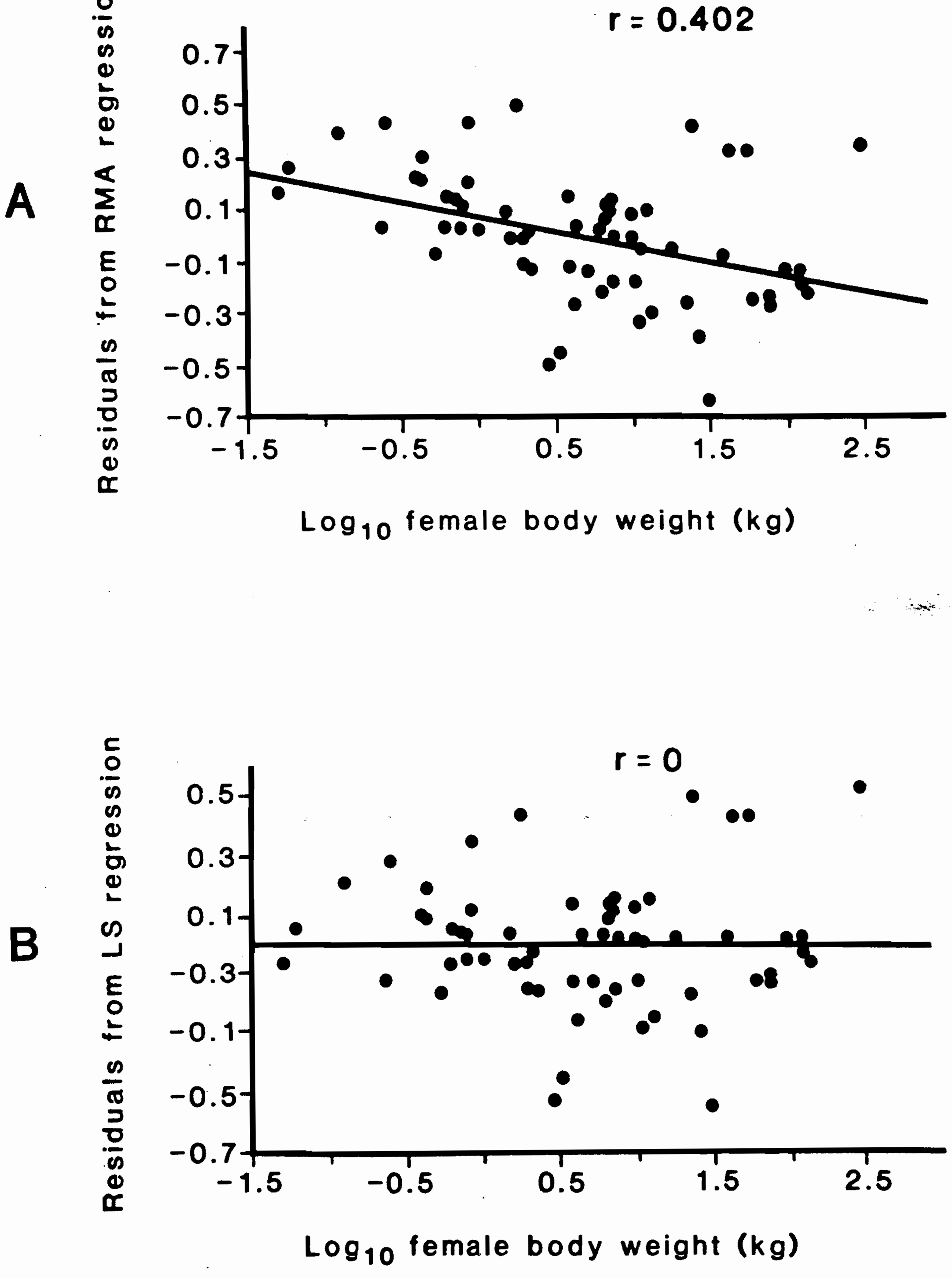
Primate Biology. Jungers, W.L. (ed.). Plenum Press, New York.

Worthy, G.A.J., and J.P. Hickie. 1986. Relative brain size in marine mammals. Amer. Nat. 128: 445-459.

Fig.1. a. Relationship between residuals from reduced major axis regression of weaning age on female body weight and female body weight in 63 mammalian species. Data were obtained from Gittleman (1986b).

b. Relationship between residuals from least-squares regression of weaning age on female body weight and female body weight.

FIG. 1


A
r = 0.402
Residuals from RMA regression
0.7
0.5
0.3
0.1
-0.1
-0.3
-0.5
-0.7
-1.5
-0.5
0.5
1.5
2.5
Log$_{10}$ female body weight (kg)
B
r = 0
Residuals from LS regression
0.5
0.3
0.1
-0.3
-0.1
-0.5
-0.7
-1.5
-0.5
0.5
1.5
2.5
Log$_{10}$ female body weight (kg)

CHAPTER 3

SEXUAL SIZE DIMORPHISM AND PHENOTYPIC VARIABILITY

ABSTRACT

A literature review has shown that phenotypic variability as measured by the coefficient of variation (CV) is related to sexual size dimorphism in organisms as varied as insects, deer, and primates. Using literature data, a study of 279 bird species has shown that males of species highly sexually dimorphic in tail length were more variable than those of species with little or no sexual size dimorphism for this trait. This same effect was also found in females, though to a lesser degree. No such trends were found in wing length, a trait reaching less extreme degrees of sexual dimorphism. Finally, tail length CV was found to be in general greater than wing length CV. It is shown how the high variability exhibited by sexually dimorphic characters could have in some cases its origin in positive allometry with body size.

INTRODUCTION

Documentation of phenotypic variation within populations is central to many fields of population biology, including population genetics, life history theory, and quantitative morphometry (e.g. Lewontin 1984; Heywood1986; Arnold and Wade 1984; Yablokov 1974). While there are many theories (largely untested) of why and how variation should exist within populations (e.g. Caswell 1978, 1983; Gillespie 1977; Lively 1986; Real 1980; Smith-Gill 1983), there are relatively few well established empirical generalizations about phenotypic variability. Yablokov (1974), in his extensive review of phenotypic variability in mammals, showed that some characters tend to be consistently more variable than others. Variability in a given character can also differ among species. Thus, Andersen and Nilssen (1983) showed that body size is more variable in free-living than in tree-boring beetles. Darwin (1896: 184-189) first proposed the rule that "highly developed" organs, and especially secondary sexual characters, tend to be highly variable within species. Since then , high phenotypic variability in sexually dimorphic characters has been noted sporadically in a variety of organisms (see review below). In the present paper, we shall first review the published evidence for the existence of a general relationship between phenotypic variability and sexual size dimorphism in metric traits. Secondly, we examine this hypothesis using an extensive data set collected from the ornithological literature.

LITERATURE REVIEW

In this section , we review some of the existing literature data on phenotypic variability of sexually dimorphic metric traits.

"Horns" of Insects and Mammals.

In a number of Horned Beetle species (*Coleoptera*) and in Earwigs

(*Dermoptera*), males have enlarged mandibules or *cerci* (Bateson and Brindley 1892). Strikingly high male variability for these traits has been documented and studied by Bateson and Brindley (1892), Gadgil (1972), and Eberhard (1982), who have found that many, but not all species have bimodal distributions for these characters (Otte and Stayman 1977). The Coefficient of Variation (CV = 100 * Standard Deviation / Mean) is a standard measure of variability that allows comparison of species with different mean values (Van Valen 1978). We have calculated or collected from the literature CVs of "horn" length and of body length (sum of pronotum and abdomen lengths) for a number of Horned Beetle species and Earwigs (Table 1). In all species for which these two measures were available, horn length CV exceeded that of body length (mean paired difference of the CVs of the two characters =17.0, s.e. =1.91, n = 12, p <0.001). Therefore, horn size, which shows a higher degree of sexual dimorphism than body length in these Horned Beetles (Otte and Stayman 1977), is also more variable than body length in males. Since female measurements could not be obtained, it was impossible to investigate whether a high phenotypic variability would also be characteristic of females. An analogous case was reported by Gould (1974), who showed that in the extinct Irish Elk, antler length CV greatly exceeded that of skull measurements like basal skull length (Table 1).

Primate Skeletal Measurements

Using Wood's (1976) and Leutenegger and Larson's (1985) data on primate skeleton, it is possible to ask whether the high variability found in highly sexually characters is limited to the males or is found in both sexes. In eight of the nine species included in these two studies, average male size for a suite of characters was greater than average female size. In these same eight species, mean CV was higher in males than in females. Only in *Callithrix jacchus* , the species in which average size in females is greater than in males, did mean female CV exceed mean male CV. This result suggests that sexual dimorphism in size and in phenotypic variability are related and that this trend is also applicable to cases of "reversed" sexual size dimorphism (females larger than males). Next, we investigated whether a functional relationship existed between sexual dimorphism in size and sexual difference in variability. Regression analysis showed no significant relationship ($p > 0.05$) between sexual dimorphism in size and in CV (Figure 1). However, if *Cebus albifrons* is excluded from the analysis, a highly significant relationship appears ($r^2 = 0.95$; $p < 0.001$). The large difference in CV between the two sexes observed in *Cebus albifrons* was attributable to the high variability of males, rather than to the low variability of females. This can be shown by comparing CVs in *Cebus albifrons* (average size dimorphism 1.05; average male CV 8.74; average female CV 4.64) to another species with approximately the same degree of sexual size dimorphism, *Saimiri sciureus* (average size dimorphism 1.03; average male CV 5.00; average female CV 4.90). It should be noted that the sample sizes in Leutenegger and Larson are relatively small (8-14 for males of *C. albifrons*) and the high CV observed in male *C. albifrons* could be due to the inclusion of an extreme individual in the data set. However, since it is difficult to argue for the *a posteriori* exclusion of this species from the analysis, the interpretation of this result remains unclear. Gingerich and Schoeninger (1979) analyzed data on tooth size variability in 48 species of non-human primates. They showed that teeth which are the most dimorphic, usually the canines and incisors, are generally more variable than less dimorphic teeth such as molars. However their measure of tooth size variability was defined as the average of male and female CVs. It is therefore impossible to attribute the high variability found in canines to one sex only.

Tail Length in Birds of Paradise.

Lecroy (1981) lists tail length mean and standard deviation for male and females in a number of sexually dimorphic species of Birds of Paradise. Male data were analyzed separatedly as plumed and unplumed ("drones") groups and no data for the whole population were given. For this reason, male and female phenotypic variabilities cannot be meaningfully compared. The mean tail lengths for the two male groups usually differed by as much as one standard deviation. This suggests that if the whole male population were analyzed as a unit, male would have higher CV than females.

In conclusion, the data presented in this section support the hypothesis of a relationship between phenotypic variability and sexual dimorphism. However some shortcomings can be readily identified. First, in some cases data on female phenotypic variability is not available and it is therefore impossible to investigate whether the high variability associated with sexual size dimorphism is sex-limited or not. This limitation is either due to failure to report female values, as in the insect data, or to the nonexistence of the character in females, as in the case of the Irish Elk's antlers , or to data presentation that prevented the extraction of male and female CVs, as in the cases of primate teeth and the tails of Birds of Paradise. The result of the analysis of the primate skeleton data was encouraging, but the number of species was rather low and the inclusion of one species, *Cebus albifrons*, removed any trend existing between sexual differences in phenotypic variability and sexual size dimorphism.

HYPOTHESES

The general hypothesis of a relationship between size dimorphism (with males larger than females) and phenotypic variability can be divided into five separate testable hypotheses as follows:

1- For a given trait, the males of highly sexually dimorphic species should show greater phenotypic variability than those of species with little or no dimorphism.

2- In sexually dimorphic species, variability should be higher in males than in females, for traits expressed in both sexes.

3- Female variability should be no higher in highly dimorphic species than in species with little or no sexual dimorphism.

4- No sexual difference in variability should be observed in species with little or no sexual dimorphism.

5- Male variability should be higher in traits with high sexual dimorphism than in traits that show little or no sexual dimorphism.

The ideal data set for testing these five hypotheses would include a large number of species, with very different degrees of sexual size dimorphism. Measurements should be available for both sexes and, to establish the generality of the results, several taxonomic orders should be included in the study. The ornithological literature provides such an opportunity as quantitative measurements, together with variability statistics are routinely recorded and published. In the next section, we present an analysis of the relationship between sexual size dimorphism and phenotypic variability in 279 species of birds.

METHODS

Scaling of Sexual Size Dimorphism

The degree of sexual size dimorphism, as measured by the ratio of male to female mean values, has been shown to be positively correlated with body size in very different taxonomic groups (arthropods and birds: Rensch 1960; Bovidae and Macropodidae : Jarman 1983; primates: Leutenegger 1982; Galliformes : Collins and Abplanalp 1968). In some groups of birds of prey, however, sexual size dimorphism is greater in the smaller species (Amadon 1975). The existence of such correlations complicates comparisons of sexual size dimorphism between species of different sizes, as any observed difference in sexual dimorphism could only be due to a difference in body size. To overcome this problem, an index of sexual size dimorphism independent from size effects is desirable.

Leutenegger (1982) described the size dependence of sexual dimorphism in primates with an allometric equation of the form:

$$\log10 \text{ male mean} = a*\log10 \text{ female mean} + \log10 b \qquad (1)$$

The value of the slope, a, indicates whether sexual dimorphism increases ($a > 1$) or decreases ($a < 1$) with mean female size, or is independent from it ($a = 1$). The advantage of this method of analysis is that for any slope value, the residual deviation from the regression line (observed $\log_{10}$ male size - expected $\log_{10}$ male size) for each species constitutes an index of sexual size dimorphism independent of body size. In the present study, both this index of sexual dimorphism and the usual index (the ratio of male to female sizes) will be used in different analyses.

Scaling of Phenotypic Variability

The quantitative analysis of phenotypic variability poses a problem similar to that of sexual size dimorphism. When species or traits of different sizes are compared it is usually found that standard deviation and the mean are strongly positively correlated (Yablokov 1974). For this reason, the Coefficient of Variation (CV = 100* SD/Mean) is usually chosen as a measure of variability corrected for the effect of the mean (Van Valen 1978). However, Yablokov (1974) has shown in his exhaustive review of CVs in various mammalian characters that CV tends to be smaller in larger traits. This suggests that in the study of variability, one should be careful to identify and correct possible size effects. As in the case of the scaling of sexual dimorphism, an allometric equation of the form:

$$\log_{10} \text{ standard deviation} = c * \log_{10} \text{ mean} + \log_{10} d \qquad (2)$$

was used to achieve this goal. Again, the slope, c, indicates whether the ratio SD/Mean, or CV/100, increases ($c > 1$) or decreases ($c < 1$), or is independent from the mean ($c = 1$). For any slope, residual deviations from the regression line constitute scaled indexes of phenotypic variability (abbreviated as PV index).

Several statistical methods have been proposed to estimate the parameters of bivariate relationships such as equation 2 [e.g. least-square regression analysis, major axis, and reduced major axis; see reviews by Ricker (1973); Leduc (1987)]. A question therefore arises: Which statistical model should be used in the scaling of phenotypic variability? In scaling variability, we are not so much interested in the values of the estimated parameters (slope and intercept) themselves, rather than in stastically removing the effect of the independent variable (the mean) on the estimate of variability, log SD, in our case. Essentially scaling consists of comparing the observed value of a dependent variable to its value predicted predicted from an independent variable [see Rose and Charlesworth (1981) for an example of the scaling of variation in quantitative genetics]. Scaling is achieved if such residual values are independent of the x-variable, log mean, in our case. It has been suggested that least-square regression analysis should be preferred over the other fitting methods when the goal is primarily prediction (as is the case in residual analysis) rather than description of the relationship between the variables of interest (Mark and Church 1977). Furthermore, as is shown in chapter 2, only residuals from least-square regression analysis meet the criterion of indepedence of the x-variable. For these reasons, we have used least-square regression analysis throughout the present study.

Data for two characters, wing and tail lengths, were collected for 375 species. This data set can be broken down in the following categories: 25 Apodiformes, 42 Anseriformes, 19 Charadriiformes, 1 Ciconiformes, 74 Galliformes, 19 Gruiformes, 138 Passeriformes, 2 Pelecaniformes, 1 Procelariiformes, and 54 Psittaciformes. Our method of analysis of variability calls for estimates of mean and standard deviation for both sexes of each species. While estimates for these two parameters were available for a large number of species, they proved to be difficult to obtain for a number of highly sexually dimorphic species. However, maximum and minimum values, together with sample size, were usually provided by the authors. Thus, for some species (32-36% of the total number of species depending on trait or sex), standard deviation was estimated for each sex from the range (maximum-minimum) and sample size (Snedecor and Cochrane 1967:40), and the mid-point was taken as an estimate of mean value. A separate data set for which both observed CV and CV estimated by this method was used to establish the validity of this procedure. Pooling all traits and sexes together, the relationship between oberved and estimated CVs was: observed CV = 0.878* estimated CV + 0.359 (s.e. slope =0.0193, r^2 = 0.84, n= 386). This relationship can be used to correct for slight biases introduced by the estimation from range and mid-point. However, we found that its use did not change our results in any significant way. We therefore present only the results obtained from the analysis using the CV estimated from range and sample size when standard deviation and mean were not available. Estimates of standard deviation could be obtained for 276-279 species (depending on trait and sex) after cases with sample sizes smaller than 10 were arbitrarily excluded from the analysis. Species with reversed sexual dimorphism (females larger than males) were also excluded. All measurements were converted to mm. Data sources were: Ali (1953), Ali and Ripley (1978), Bannerman (1930-51), Cheng (1964), Cramp (1977), Delacour (1977), Delacour and Amadon (1973), Forshaw (1978), Johnsgard (1973), McLachlan and Liverside (1978), Palmer (1962), and Ridgway (1901-50).

ANALYSIS AND RESULTS

Sexual Size Dimorphism

Figures 2a, and b illustrate the relationship between log male and log female mean values for tail and wing length. The relationship for tail length was weaker (r^2 = 0.81) than the wing length relationship (r^2 = 0.98), and relatively large residual deviations above the tail length regression line were evenly distributed over the whole female size range. For example, species with large sexual dimorphism in tail length ranged in size from the small Streamer-tailed Hummingbird, *Aithurus polytmus* (female mean tail length = 37 mm; male/female tail lengths = 4.45), to the larger Peacock, *Pavo cristatus* (female mean tail length = 350 mm;male/female tail lengths = 4.29). Sexual dimorphism in wing length did not reach such extremes, with virtually all species (365/373) had sexual dimorphism (male mean/female mean) between 1 and 1.5. The two outliers at the top right corner of figure 2b are sub-species of the Great Argus (*Argusianus argus argus* and *A. a. grayi*) in which wing length reaches high degrees of sexual dimorphism (male/female midpoints respectively 2.40 and 2.73). In these peacocks, the wing feathers instead of the tail feathers (as is usually the case in peacocks) are primarily used in display (Delacour 1977). In 74 species (20 %), tail length sexual dimorphism exceeded 1.5, and, in some species, reached values between 2 and 8. The tail length data therefore allow us to compare species with very different degrees of sexual dimorphism. Wing length appears to be a more conservative trait than tail length, reaching only modest degrees of sexual size dimorphism. For this reason, we expect it to be less variable than tail length (prediction 5).

For both trait, the slopes of the regressions of log male mean on log female mean were not significantly different from unity (Table 2). There is therefore no indication of the existence of a tendency for sexual size dimorphism to change with size in these two characters. Finally, tail length dimorphism and wing length dimorphism were poorly (even though significantly: $r^2 = 0.11$, $p<0.001$) correlated (Fig. 3), so that comparisons involving the two traits will not be redundant.

Phenotypic Variability

Figures 4a-d show the bivariate relationships between log SD and log Mean for each sex and trait combination. For the tail length data, significant departures of the regression slopes from the value of 1 were found in both sexes (Table 3). For this trait, phenotypic variability, if measured by CV, would therefore tend to increase in larger species. As pointed out above, the residual deviations from the regression lines constitute indexes of phenotypic variability (abbreviated as PV index) that are free from these scaling problems. Except when indicated, this index will be used in subsequent analysis in the present paper. No significant departures from a slope of 1 were found in either sex in the wing length data. Thus species with long wings did not show higher variability (CV) than small species.

Relationship between Sexual Dimorphism and Phenotypic Variability

First, the relationship between PV index and sexual size dimorphism indexes was investigated for the four sex/trait combinations (predictions 1 and 3; Figures 5a-d). Species were separated into two groups according to their degree of sexual size dimorphism: those with positive sexual dimorphism index, and those in which this index was equal to or smaller than zero. Thus the first group included the most sexually dimorphic species, and the second, the species with less or no sexual dimorphism. For each sex/trait combination, PV indexes were then compared between the two groups with a non-parametric Wilcoxon Rank-Sum T-test (Snedecor and Cochran 1967) . As expected (prediction 1), tail length among males of the high dimorphism group was found to be significantly more variable that among those in the low dimorphism group (Table 3). This is also illustrated in Figure 5a which show that the species at the right of the vertical line situated at sexual dimorphism = 0 tend to lie more above the horizontal line at PV = 0 then the species of the low sexual dimorphism group. There are few species in the low dimorphism group with PV index values as high as those from the high dimorphism group. Thus it appears that the observed difference in PV index between the two groups can be explained by a deficit in the number of species having both high sexual dimorphism and low PV index. The same pattern was observed in the female tail length data (Fig. 5b and Table 3), as female tail length was more variable in the highly dimorphic group than in those with little or no sexual dimorphism. Thus the high phenotypic variability associated with high sexual size dimorphism was not found to be limited to the male sex, as was we predicted (prediction 3).

For wing wing length data (Fig. 5c and d and Table 3), no significant differences in PV index between species with different degrees of sexual size dimorphism were found in either sex. For this character, therefore, phenotypic variability is not influenced by sexual size dimorphism.

These results are only partly consistent with our predictions. The association between high phenotypic variability and high sexual dimorphism was observed in both sexes in the tail length, rather than in the male alone, supporting prediction (1), but rejecting prediction (3). Nevertheless, males in highly dimorphic species might still be more variable than females (prediction 2). We tested this possibility by calculating the difference in CV between the two sexes for each trait/sexual dimorphism group combination. No significant sexual difference in CV was found among the four combinations of trait and sexual dimorphism groups (Table 4). For wing length, and for the group with low sexual dimorphism in tail length, these results confirmed our prediction that no sexual sexual difference in variability should be observed in species (or traits) with little or no sexual size dimorphism (prediction 4). Although the highest sexual difference in CV was found in the case of the group with high sexual dimorphism in tail length, this result was not significant, and did not confirm our second prediction.

Finally, we predicted that characters with high levels of sexual size dimorphism should be more variable than more conservative traits (prediction 5). We therefore expected tail length CV to be greater than wing length CV. Pooling the data for all species, it was found that male tail length CV nearly averaged twice the value of male wing CV (5.20 vs 2.65) (Fig. 6). In both sexes, the averaged paired difference in CV between the two traits was significant (Table 5).

DISCUSSION

The principal result of the present study were: first, that males of highly sexually dimorphic species were more variable than males of species with little or no sexual dimorphism, and secondly, that tail length was both more variable and more sexually dimorphic than wing length. These two results confirmed the fragmentary evidence summarized in the review section. They do not, however, shed any light on the problem of the nature of this high variability. CV, or any other single-parameter measure of variability, contains much less information than is present in the original character frequency distribution. In fact, it is possible to imagine frequency distributions having very different shapes but the same means and CVs. Two such distributions are shown in Figure 7. The bimodal distribution corresponds to Batesons and Brindley's (1892) data on horn size in males of the Horned Beetle *Xylotrupes gideon* . The unimodal distribution is an hypothetical case which will be referred to below. Although they show the same level of variability, as indicated by their same CVs, these curves represent quite different phenomena which call for different explanations. These two modes of variation will be considered in the following discussion of our results in relation to various hypotheses of sexual selection.

Genetic models of sexual selection stress the fact that evolution of sexual size dimorphism is only possible if some genetic variation is present. Furthermore, the greater the amount of genetic variation present, the greater the rate of advance under selection will be. A difference in the amount of genetic variation between the two sexes may lead to a sexual difference in size, even if the selection intensity on size is the same in both sexes. This idea can be traced back to Darwin's (1896: 185-189) notion of "generative variability". Briefly, a great modification implies that high levels of variation have been maintained for long periods of time. If the selection period has not been excessively long, we might then expect some variability to persist. Essentially, this is the same point that was later made by Leutenegger and Cheverud (1985), who proposed that sexual size dimorphism in primates can be explained by sexual differences in the amount of genetic variation present in the two sexes. Under this hypothesis, high variability is not the consequence of the selection for sexual dimorphism but rather its cause. One problem with this theory is how long, under continuous selection, the difference in genetic variation would persist. This model also begs the question of why males should be more variable than females in the first place.

However, in the majority of quantitative genetics model of sexual selection, the direction of the causation between sexual dimorphism and variability is reversed, with high genetic variation being viewed as the potential result of sexual selection on the male character. O'Donald's (1980) comprehensive book reviews the various sexual selection models leading to genetic polymorphisms in male traits. His conclusion is that the existence of stable polymorphisms for secondary sexual characters depends on specific aspects of the genetic models, such as the nature of genetic variation (e.g dominance or recessivity of the male trait), and the type of frequency dependence of female choice. Thus, these models could in principle explain the existence of bimodal distributions such a were observed in male secondary sexual characters in insect species (Bateson and Brindley 1892; Otte and Stayman 1977).

Some workers (Eberhard 1982; Kodric-Brown and Brown 1984; Nur and Hasson 1984) have suggested that the development of secondary sexual characters might be a response to internal condition such as overall health or vigor, or to external factors such as social status. Adult body size may be an important correlate of such factors (Nur and Hasson 1984). Under this hypothesis, the size of a secondary sexual character should be positively correlated to body size, and its variability will then reflect that of body size. However, it is not clear why secondary sexual characters should generally be more variable than body size, as our results suggest.

This difference in variability can be explained by the fact that a high CV in a particular character Y can be the simple result of a correlation with another, less variable, character X. Given an initial frequency distribution of X, with CV_x , CV_y will depend on the shape of the relationship between Y and X. If the relationship is concave, so that the ratio Y/X increases with X, then CV_y will be greater than CV_x . The allometric equation, $Y = bX^a$, has been traditionally used to describe the relationships between various morphometric characters in a wide array of organisms (Huxley 1972; Thompson 1961). If the allometric coefficient, a, is greater than 1 ("positive allometry"), the relationship between Y and X is concave, and CV_y will be greater than CV_x . We have found in numerical studies that the ratio CV_y/ CV_x is approximately given by a, when $CV_x < 30\%$. With higher CV_x and non-normal distribution of X, the relationship between CV_y / CV_x and a becomes less precise; however, CV_y/ CV_x always exceeds 1, provided that a is greater than 1. If the higher variability found in secondary sexual characters has its origin in allometric relationships with other less variable characters, particularly body size, we would expect that the majority of documented allometric relationships between such traits and body size measurements should show positive allometry.

Rensch (1960) was the first to suggest that "display" organs like antlers, crests and tails often have positive intraspecific allometry with body size. Otte and Stayman (1977) reported positive allometry between male horn size and body size in a number of Horned Beetle species. Hartnoll (1974) studied the allometry between claw size and carapace size in the males and females of 24 species of crabs. In these species, one claw is much larger in the male than in the female and is used by the males as a display organ. The average allometric coefficient, a, was larger larger in the males than in the females both before (1.26 *vs* 1.11), and after puberty (1.53 *vs* 1.10). In some species of the lizard genus *Anolis* , males have a dewlap, which is a display organ situated under the throat; females have small dewlaps or none. Echelle et al (1978) found positive allometry between dewlap size and body size in all the 21 species that they studied. Positive allometry between antler size and body or skull size measurements have also been reported in deer (Huxley 1931; Anderson and Medin 1969; Gould 1974).

These studies clearly support Rensch's (1960) generalization that positive allometry is common in secondary sexual characters. If the high variability showed by secondary sexual characters has its origin in such positive allometry, then we may ask why, in the first place, positive allometry between such traits and body size should be the rule. Kodric-Brown and Brown's (1984) "truth in advertisement" hypothesis might provide a clue. They proposed that "sexual selection favors the evolution of costly, phenotypically variable traits whose expression reflects the survivorship and vigor of males and hence their overall genetic quality". They also point out that the reliability of the advertising trait as an indicator of genetic quality is proportional to the degree of its positive covariance with it. Here we might add that two aspects of this reliability can be distinguished. First, as Kodric-Brown and Brown (1984) emphasized, the advertising traits (abbreviated as trait A from now on) should be costly, so that "cheating" by some males is impossible, and therefore the variation in trait A accurately reflects variation in male quality. A second aspect in the reliability of an advertising trait, not mentioned by Kodric-Brown and Brown (1984), is its precision or resolving power. Even if a trait A is prefectly correlated with male quality, female choice based on variation in trait A will be possible only to the extent that there exists a sizeable variability for this character. As we have seen above, positive allometry between trait A and body size has the effect of increasing the CV of trait A compared to that of body size. The relative difference in trait A between any two males will therefore be higher than their relative difference in body size. Hence, positive allometry acts as a sort of magnifier of differences in male quality. Discrimination ability in female choice is probably an important aspect of their mating strategy. For example, Wooton et al (1986) presented a modified version of Orians (1969) polygyny-threshold model in which female mating strategy (monogamy or polygyny) is influenced by the importance of errors in the estimation of male quality (in their case, territory quality).

By definition, positive allometry between trait A and body size also means that the ratio of trait A size/body size increases with body size. If one accepts that this ratio is proportional to the costs incurred by the male, it follows that positive allometry entails a cost which increases with male body size (a correlate of male quality, as we assumed), therefore meeting the first requirement of reliability in the "truth in advertisement" hypothesis: that the cost of advertising prohibits "cheating". Thus , according to this view, sexual selection creates high phenotypic variablity in secondary sexual characters through positive allometry. Our results suggested that the high variability associated with sexual dimorphism was not limited to the male only, but was also expressed in female tail length. Atchley et al (1981) have shown that in rodents the patterns of covariance among metric characters are themselves heritable. If high variability found in males of highly dimorphic species is due to genes determining positive allometry, the females could also exhibit high variability if the effets of such genes are not entirely sex-limited.

Positive allometry also has the effect of increasing the degree of skewness in character Y compared to that of character X. The reason for this is that positive allometry is essentially a power transformation of body size with an exponent greater than 1. For example, the skewed unimodal distribution in Figure 7 was generated by raising each observation of an initial normal distribution to the fourth power. Such a unimodal and positively skewed distribution model is therefore more compatible with the allometric explanation of phenotypic variability than the bimodal model is. However, the two models are not incompatible, as positive allometry can accompany bimodality in some Horned Beetles (Otte and Stayman 1977). Only with complete data sets, rather that only mean and standard deviation, will it be possible to evaluate the relative importance of the two types of distributions as general explanation of the high variability of secondary sexual characters.

LITERATURE CITED

Andersen, J., and A.C. Nilssen. 1983. Intrapopulation size variation of free-living and tree-boring Coleoptera. Can J. Ent. 115: 1453-1464.

Anderson, A.E., and D.E. Medin. 1969. Antler morphometry in Colorado Mule Deer populations. J. Wild. Manag. 33: 520.533.

Ali, A.A. 1953. The Birds of Travancore and Cochin. Oxford University Press, London.

Ali, A.A., and S.D. Ripley. 1978. Handbook of the Birds of India and Pakistan. Vol. 1-10. Oxford University Press, London.

Amadon, D. 1975. Why are female birds of prey larger than males? Raptor Res. 9: 1-11.

Arnold, S.J., and M.J. Wade. 1984. On the measurement of natural and sexual selection: Theory. Evolution 38: 709-719.

Atchley, W.R., Rutledge, J.J., and D.E. Cowley. 1981. Genetic components of size and shape. II. Multiple covariance patterns in rat and mouse skull. Evolution 35: 1037-1055.

Bannerman, D.A. 1930-51. The Birds of Tropical West Africa. Vol. 1-8. Crown Agents for the Colonies, London.

Bateson, W., and H.H. Brindley. 1892. On some cases of variation in secondary sexual characters, statistically examined. Proc. Zool. Soc. London 1892: 585-594.

Caswell, H. 1978. A general formula for the sensitivity of population growth rate of changes in life history parameters. Theor. Pop. Biol. 14: 215-230.

Caswell, H. 1983. Phenotypic plasticity in life-history traits: Demographic effects and evolutionary consequences. Amer. Zool. 23: 35-56.

Cheng, T. 1964. China's Economic Fauna: Birds. Joint Publications Research Service, Washington.

Collins, W.M., and H. Abplanalp. 1968. Change in body and organ weights of Japanese Quails selected for 6-weeks body weight. Brit. Poultry Sc. 9: 231-242.

Cramp, J. 1977. The Handbook of the Birds of Europe, the Middle East, and North Africa. Oxford University Press, Oxford.

Darwin, C.R. 1896. The Origins of Species. Vol 1. Appleton, D. and Cie, New York.

Leutenegger, W. 1982. Scaling of sexual dimorphism in body weight and canine size in primates. Folia Primat. 37: 163-176.

Leutenegger, W., and J. Cheverud. 1985. Sexual dimorphism in primates: The effects of size; in Jungers, W.L. (eds.). Size and Scaling in Primate Biology. Plenum Press, New York.

Leutenegger, W., and S. Larson. 1985. Sexual dimorphism in the post-cranial skeleton of New World Primates. Folia Primat. 44: 82-95.

Lewontin, R.C. 1984. Detecting population differences in quantitative characters as opposed to gene frequencies. Amer. Nat. 123: 115-124.

McLachlan, C.R., and R. Liverside. 1978. Birds of South Africa. Trustees of the John Vaelcher Bird Book Fund, Capetown.

Nur, N., and O. Hasson. 1984. Phenotypic plasticity and the handicap principle. J. Theor. Biol. 110: 275-297.

O'Donald, P. 1980. Genetic Models of Sexual Selection. Cambridge University Press, Cambridge.

Orians, G.H. 1969. On th evolution of mating systems in birds and mammals. Amer. Nat. 103:589-603.

Otte, D., and K. Stayman. 1977. Beetle Horns: Some patterns in functional morphology. p. 259-292. In "Sexual Selection and Reproductive Competition in Insects. Blum, M.S., and N.A. Blum (eds.). Academic Press, New York.

Palmer, R.S. 1962. Handbook of the American Birds. Yale University Press, New Haven.

Real, L.A. 1980. Fitness, uncertainty, and the role of diversification in evolution and behavior. Amer. Nat. 115: 623-638.

Rensch, B. 1960. Evolution above the Species Level. Columbia University Press, New York.

Ridgway, R. 1901-50. The Birds of North and Middle America. Vol. 1-11. Government Printing Office, Washington.

Rose, M., and B. Charlesworth. 1981. Genetics of life history in *Drosophila melanogaster*. I. Sib analysis of adult females. Genetics 97: 187-196.

Smith-Gill, J. 1983. Developmental plasticity: Developmental conversion *versus* phenotypic modulation. Amer. Zool. 23: 47-55.

Snedecor, G.W., and W.G. Cochran. 1967. Statistical Methods. Iowa State University Press, Iowa.

Nat. Hist. Novit. 2714: 1-52.

Leutenegger, W. 1982. Scaling of sexual dimorphism in body weight and canine size in primates. Folia Primat. 37: 163-176.

Leutenegger, W., and J. Cheverud. 1985. Sexual dimorphism in primates: The effects of size; in Jungers, W.L. (eds.). Size and Scaling in Primate Biology. Plenum Press, New York.

Leutenegger, W., and S. Larson. 1985. Sexual dimorphism in the post-cranial skeleton of New World Primates. Folia Primat. 44: 82-95.

Lewontin, R.C. 1984. Detecting population differences in quantitative characters as opposed to gene frequencies. . Amer. Nat. 123: 115-124.

Mark, D.M., and M. Church. 1977. On the misuse of regression in earth science. Math. Geol. 9: 63-75.

McLachlan, C.R., and R. Liverside. 1978. Birds of South Africa. Trustees of the John Vaelcher Bird Book Fund, Capetown.

Nur, N., and O. Hasson. 1984. Phenotypic plasticity and the handicap principle. J. Theor. Biol. 110: 275-297.

O'Donald, P. 1980. Genetic Models of Sexual Selection. Cambridge University Press, Cambridge.

Orians, G.H. 1969. On th evolution of mating systems in birds and mammals. Amer. Nat. 103:589-603.

Otte, D., and K. Stayman. 1977. Beetle Horns: Some patterns in functional morphology. p. 259-292. In "Sexual Selection and Reproductive Competition in Insects. Blum, M.S., and N.A. Blum (eds.). Academic Press, New York.

Palmer, R.S. 1962. Handbook of the American Birds. Yale University Press, New Haven.

Real, L.A. 1980. Fitness, uncertainty, and the role of diversification in evolution and behavior. Amer. Nat. 115: 623-638.

Rensch, B. 1960. Evolution above the Species Level. Columbia University Press, New York.

Ricker, W.E. 1973. Linear regressions in fishery research. J. Fish. Res. Brd. Can. 30: 409-434.

Ridgway, R. 1901-50. The Birds of North and Middle America. Vol. 1-11. Government Printing Office, Washington.

Smith-Gill, J. 1983. Developmental plasticity: Developmental conversion *versus* phenotypic modulation. Amer. Zool. 23: 47-55.

Snedecor, G.W., and W.G. Cochran. 1967. Statistical Methods. Iowa State University Press, Iowa.

Sokal, R.R., and F.J. Rohlf 1981. Biometry. 2nd ed. Freeman, San Fransisco.

Thompson, D.W. 1961. On Growth and Form. J.T. Bonner, ed. Cambridge University Press, Cambridge.

Van Valen, L. 1978. The statistics of variation. Evol. Theor. 4: 33-43.

Wood, B.A. 1976. The nature and basis of sexual dimorphism in the primate skeleton. J. Zool. 180: 15-34.

Wooton, J.T., Bollinger, E.K., and C.J. Hibbard. 1986. Mating systems in homogeneous habitats: The effects of female uncertainty, knowledge costs, and random settlement. Amer. Nat. 128: 499-512.

Yablokov, A.V. 1974. Variability in Mammals. Amerind, New Delhi.

1

Table 1. Coefficients of variation for sexually dimorphic characters and body size measurements in 15 species of Horned Beetles, Earwig (*Forficula auricularia*), and the Irish Elk (*Megaloceros giganteus*). CVs for Otte and Stayman's (1977) data were calculated as estimated standard deviation/midpoint (in %). Standard deviations were estimated from range and sample size (Snedecor and Cochrane 1967:40), which were themselves estimated from figures in their paper. CVs from Bateson and Brindley (1892) were calculated by extracting the data from a frequency distribution histogram. Gould (1976) directly reported values of CVs.

TABLE 1

THE PHENOTYPIC VARIABILITY OF SEXUALLY DIMORPHIC CHARACTERS

SPECIES	TRAIT CV (%)	TRAIT CV (%)	SOURCE
	INSECTS		
	Mandibule Length	Body Length	
Chiasognatus grantii	23.8	6.1	1
Cladognatus giraffe	23.8	9.8	1
Cyclomatus platyrnelus	35.1	10.5	1
Hexarthus davisoni	23.9	17.3	1
Lamprina adolphinae	20.2	13.7	1
Lucanus cervus	31.6	11.3	1
Lucanus elephas	15.6	7.7	1
Metoporidus savagei	33.7	9.2	1
Odontabilis siva	26.4	8.4	1
Odontabilis cuvera	32.0	9.1	1
Prasapocoelus serricornis	29.9	12.9	1
Psalidamerus inclinatus	31.1	11.1	1
Serrognatus intermedius	43.3	11.8	1
Serrognatus platymelus	31.4	17.7	1
Xylotrupes gideon	37.7	-	2
	Cercus Length		
Forficula auricularia	33.5	-	2

MAMMALS

	Antler Length	Skull Length	
Megaloceros giganteus	16.6	2.7	3

Sources: 1. Otte and Stayman (1977). 2. Bateson and Brindley (1892).
3. Gould (1974).

Table 2. (a) Regression analysis of the scaling of sexual size dimorphism for tail length and wing lengths in birds. (b) Regression analysis of phenotypic variability of tail and wing lengths for both sexes. Y stands for standard deviation and X for corresponding mean tail or wing length (see Methods). T-tests [slope-1/s.e. (slope)] were used to judge the significance of the departure of the regression slopes from the value of unity. Data sources are listed in the text.

TABLE 2

REGRESSION STATISTICS

LOG Y	LOG X	SLOPE	SE	P=1?	INT.	N	R^2
A. SEXUAL SIZE DIMORPHISM							
1. Male Tail	Female Tail	1.04	0.027	>0.05	0.006	371	0.81
2. Male Wing	Female Wing	1.00	0.006	>0.05	0.003	373	0.98
B. PHENOTYPIC VARIABILITY							
3. Male Tail SD	Male Tail	1.27	0.039	<0.001	-0.88	279	0.79
4. Female Tail SD	Fem. Tail	1.11	0.051	<0.001	-1.57	275	0.63
5. Male Wing SD	Male Wing	0.98	0.061	>0.05	-1.57	276	0.82
6. Fem. Wing SD	Fem. Wing	1.00	0.033	>0.05	-1.61	274	0.77

Table 3. Comparison of phenotypic variability index between species with high sexual size dimorphism ("high group") and species with little or no sexual dimorphism ("low group") for the four trait/sex combinations. For each case, the significance of the difference in variability index between the two groups was tested with a Wilcoxon-Sum t-test (Snedecor and Cochrane 1967). The direction of the expected and observed differences in variability between the high and low groups are given for each trait/sex combination.

TABLE 3

RELATION BETWEEN PHENOTYPIC VARIABILITY AND SEXUAL SIZE DIMORPHISM

	High Dimorphism Group			Low Dimorphism Group					
TRAIT	MEAN	SE	N	MEAN	SE	N	PRED.	OBS.	P
1. Male Tail	0.035	0.041	70	-0.091	0.011	207	>	>	<0.001
2. Female Tail	0.092	0.033	70	-0.021	0.014	205	=	>	<0.001
3. Male Wing	0.008	0.013	172	0.015	0.014	104	=	=	>0.05
4. Female Wing	0.007	0.024	171	0.017	0.013	103	=	=	>0.05

Table 4. Sexual differences in CV for tail and wing lengths in highly dimorphic species ("high group") and species with less or no sexual dimorphism ("low group"). The significance of the difference in CV between the two sexes was tested with a paired Wilcoxon Rank-Sum t-test (Snedecor and Cochrane 1967).

TABLE 4

SEXUAL DIFFERENCES IN CVs

TRAIT	DIMORPHISM GROUP	MEAN	SE	N	P
1. Tail Length	Low	0.06	0.13	205	>0.05
2. Tail Length	High	0.69	0.53	70	>0.05
3. Wing Length	Low	-0.08	0.08	167	>0.05
4. Wing Length	High	-0.05	0.17	102	>0.05

Table 5. Difference in CV between tail and wing lengths for each sex. The significance of the difference in CV was tested with a paired Wilcoxon Rank-Sum t-test.

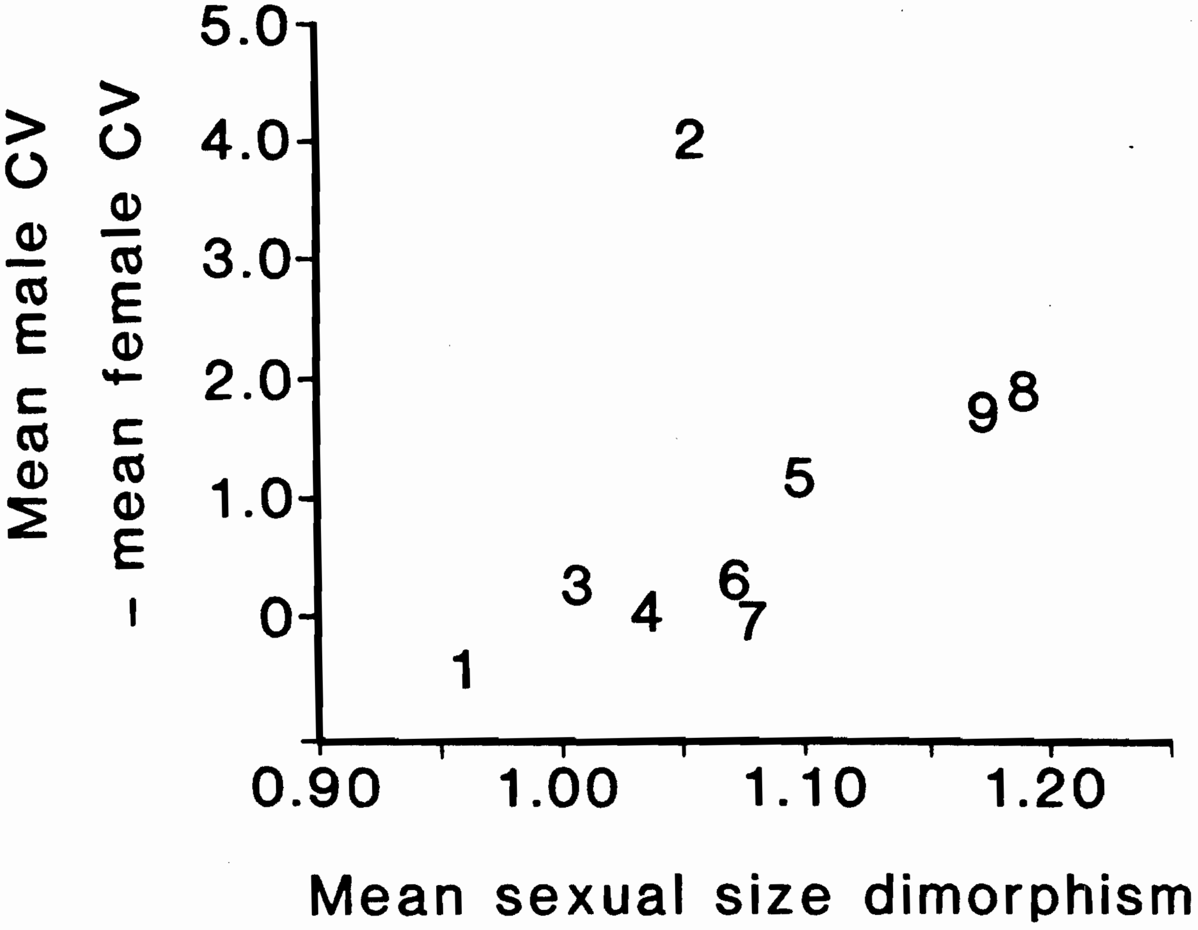
TABLE 5

PAIRED DIFFERENCE BETWEEN TAIL AND WING LENGTH CVs

SEX	MEAN	SE	N	P
1. Males	2.56	0.185	269	<0.001
2. Females	2.27	0.199	272	<0.001

Figure 1. Relationship between sexual difference in mean CV (%) and mean sexual size dimorphism (mean male value/mean female value) in skeletal measurements in primates. Data from Wood (1976) are based on measurements of 91 characters, those from Leutenegger and Larson (1985), on 19 characters. Species legend: 1- *Callithrix jacchus* , 2- *Cebus albifrons* , 3- *Saguinus nigricollis* , 4- *Saimiri sciureus* (Leutenegger and Larson 1985); 5- *Colobus guereza* , 6- *Homo sapiens* , 7- *Pan troglodytes* , 8- *Papio anubis*, 9- *Gorilla gorilla* (Wood 1976).

FIG. 1


Mean male CV
- mean female CV
5.0
4.0
3.0
2.0
1.0
0
0.90
1.00
1.10
1.20
Mean sexual size dimorphism
1
2
3
4
5
6
7
8
9

igure 2. Double logarithmic relationship between male and female mean values for (a) tail length (371 species), and (b) wing length (373 species).

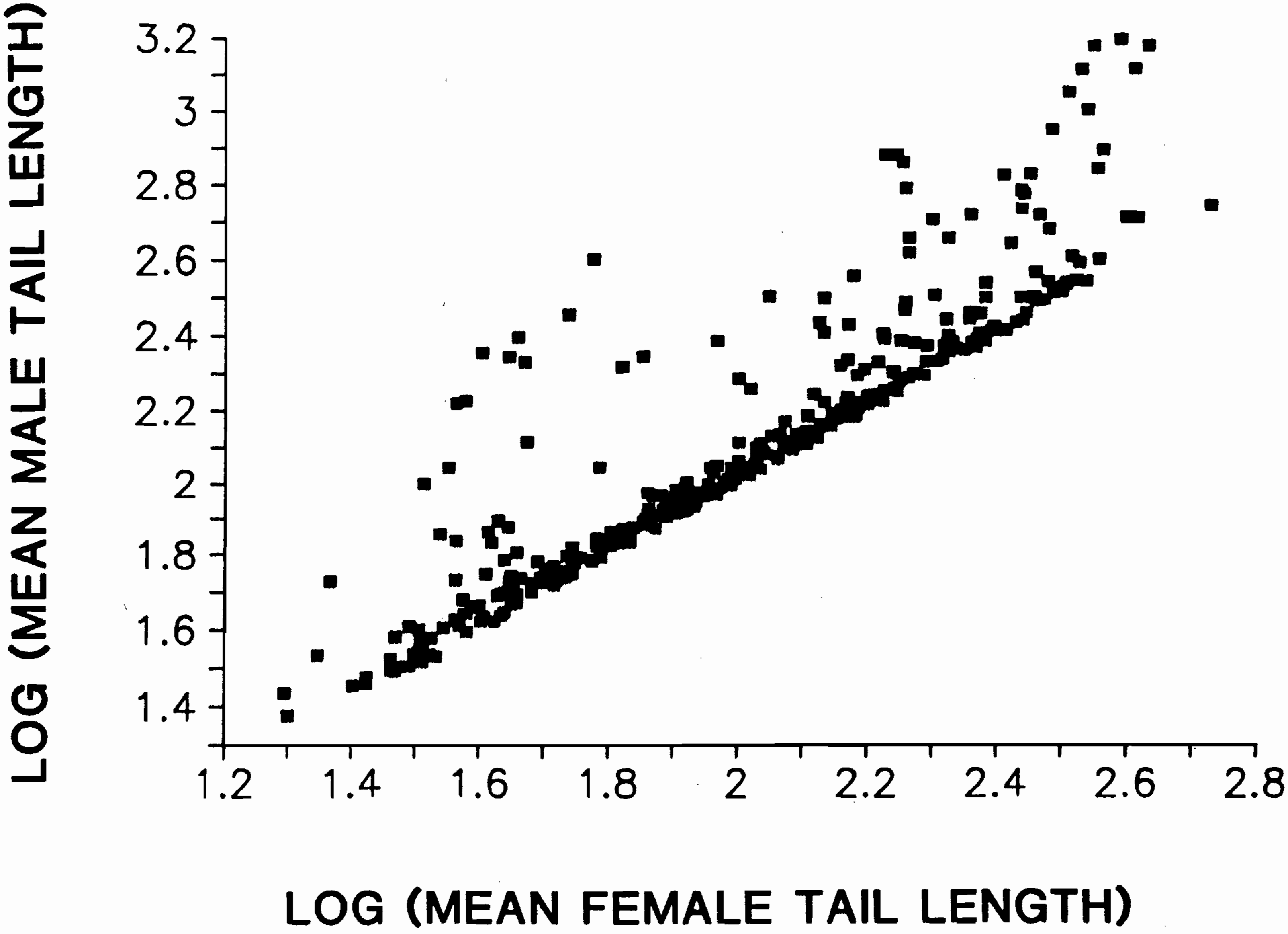

LOG (MEAN MALE TAIL LENGTH)
3.2
3
2.8
2.6
2.4
2.2
2
1.8
1.6
1.4
1.2
1.4
1.6
1.8
2
2.2
2.4
2.6
2.8
LOG (MEAN FEMALE TAIL LENGTH)

FIG.2A

FIG.2B

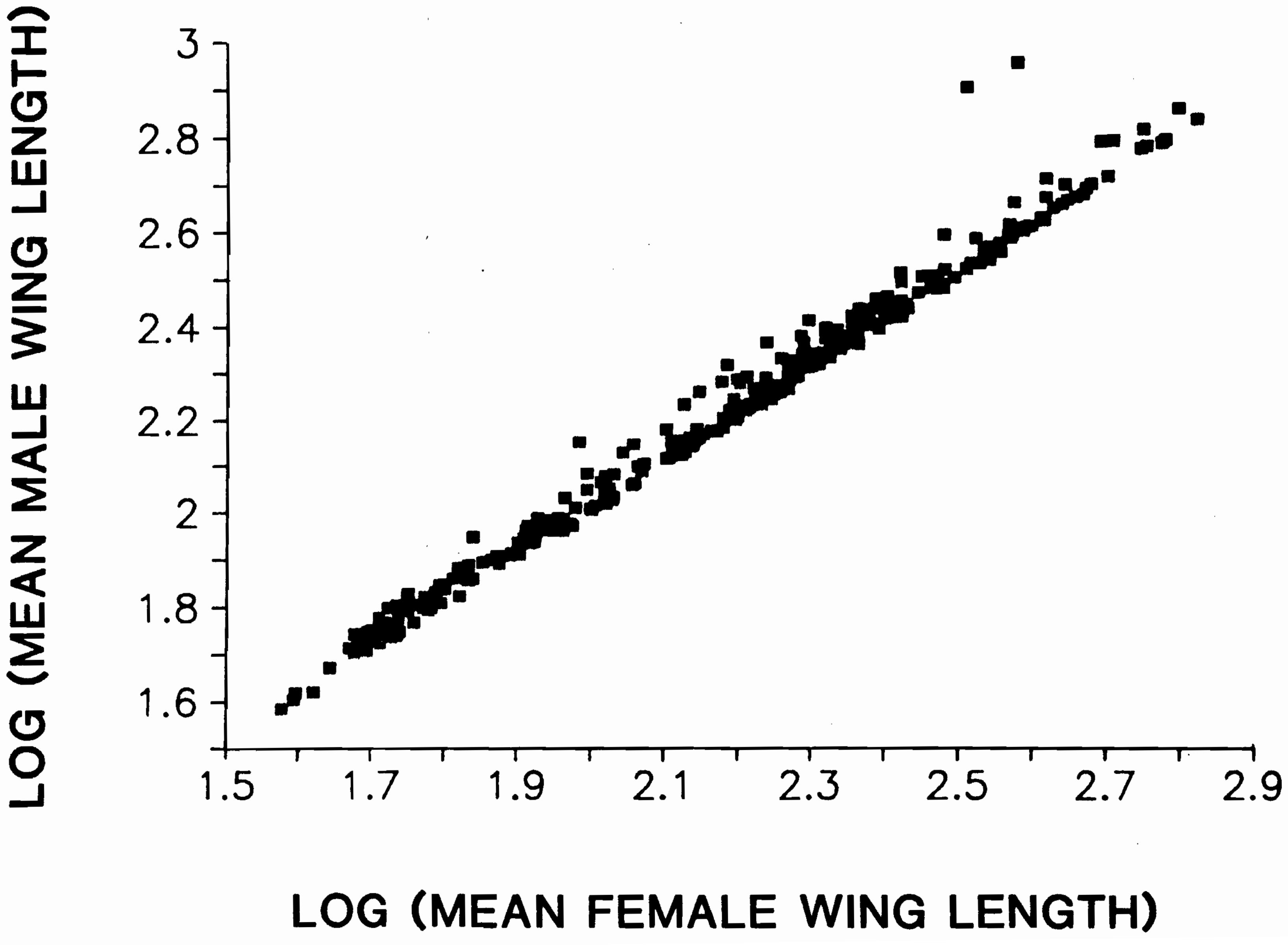

LOG (MEAN MALE WING LENGTH)
3
2.8
2.6
2.4
2.2
2
1.8
1.6
1.5
1.7
1.9
2.1
2.3
2.5
2.7
2.9
LOG (MEAN FEMALE WING LENGTH)

Figure 3. Relationship between tail length sexual dimorphism and wing length sexual dimorphism in 370 species of birds.

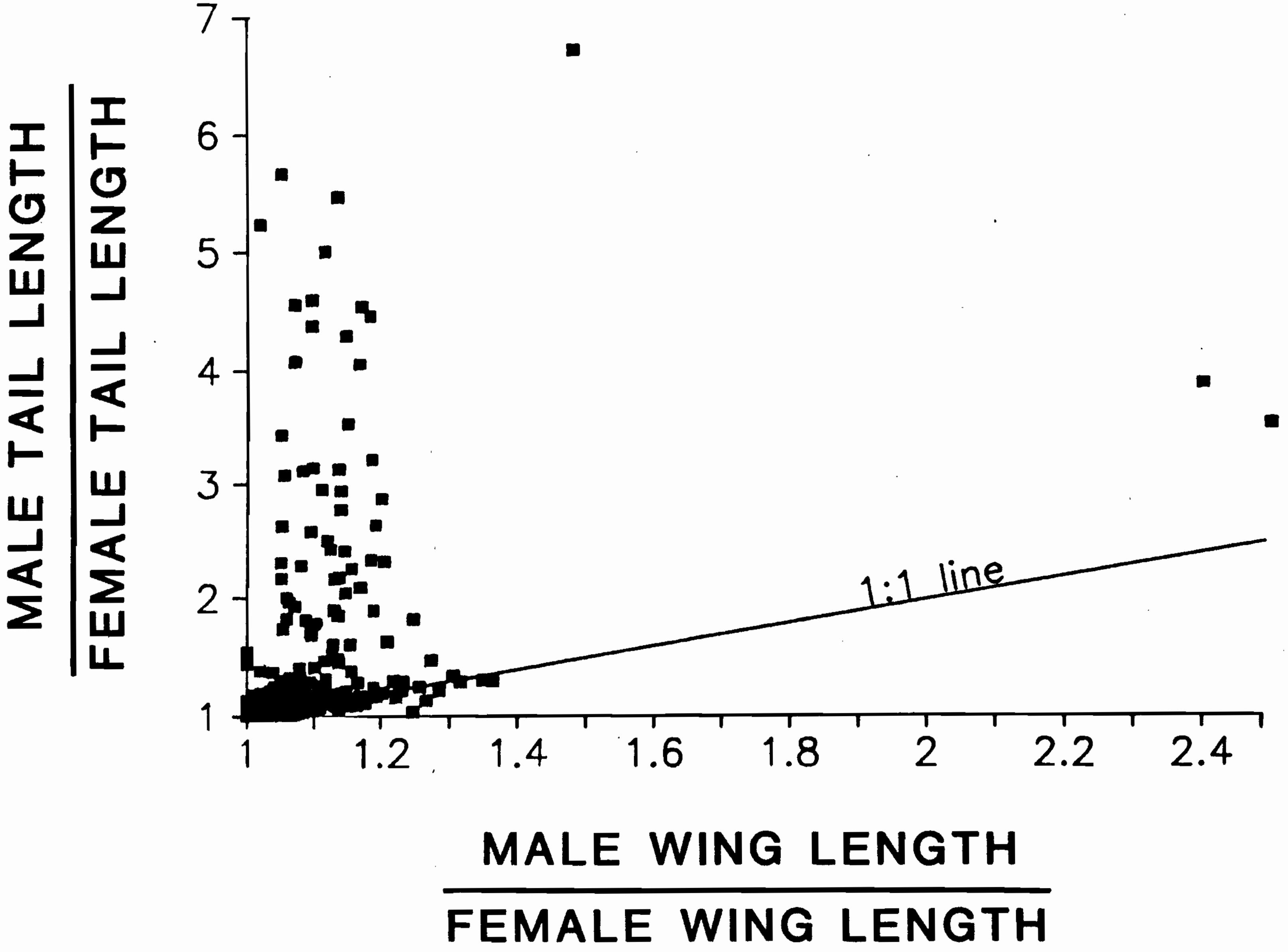

7
6
5
4
3
2
1
1
1.2
1.4
1.6
1.8
2
2.2
2.4
1:1 line
MALE TAIL LENGTH
FEMALE TAIL LENGTH
MALE WING LENGTH
FEMALE WING LENGTH

FIG.3

igure 4. Relationship between $\log_{10}$ SD $\log_{10}$ Mean for male and female tail length (4a and 4b), and male and female wing length (4c and 4d).

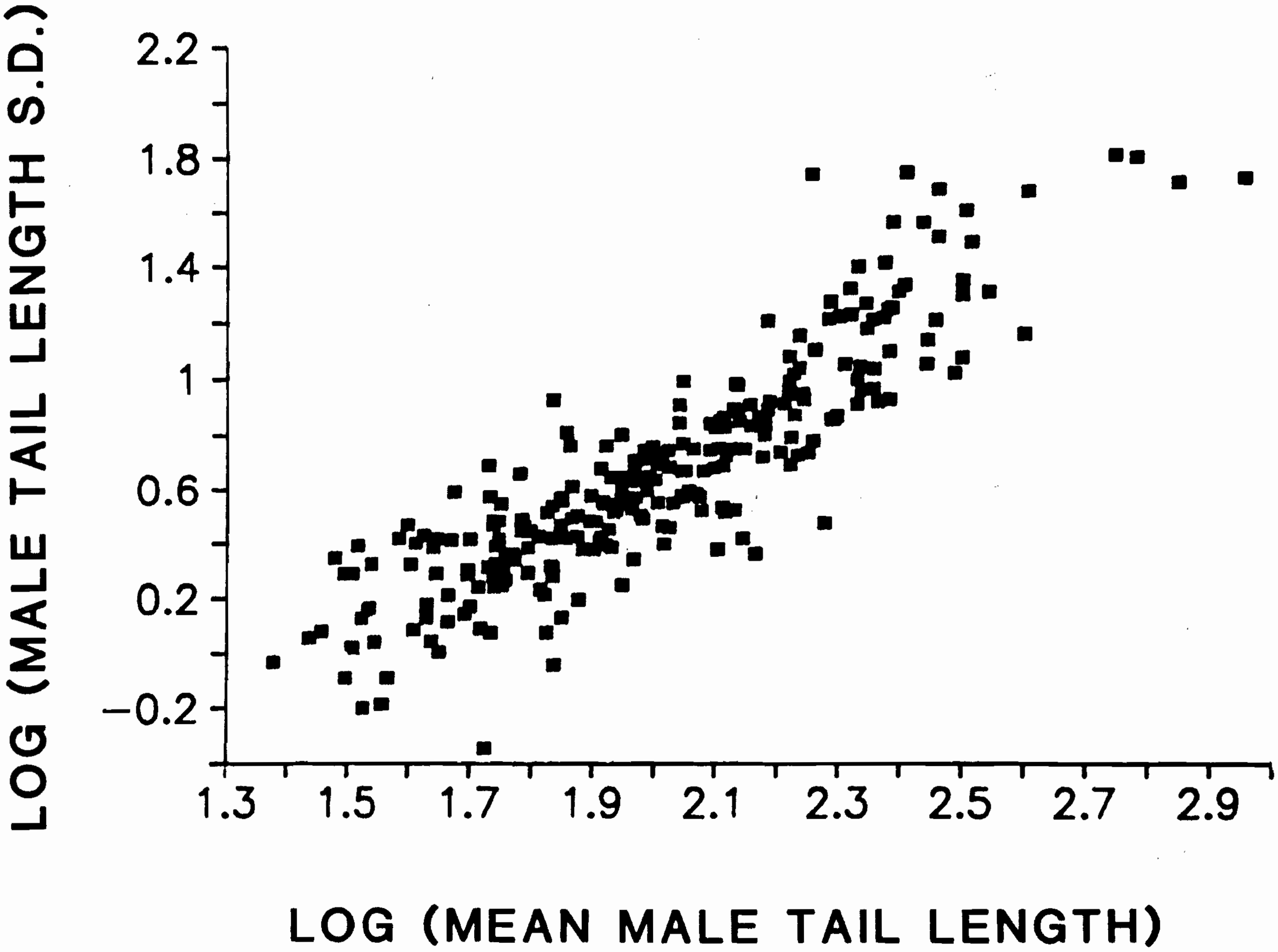

2.2
1.8
1.4
1
0.6
0.2
−0.2
1.3
1.5
1.7
1.9
2.1
2.3
2.5
2.7
2.9
LOG (MALE TAIL LENGTH S.D.)
LOG (MEAN MALE TAIL LENGTH)

FIG.4A

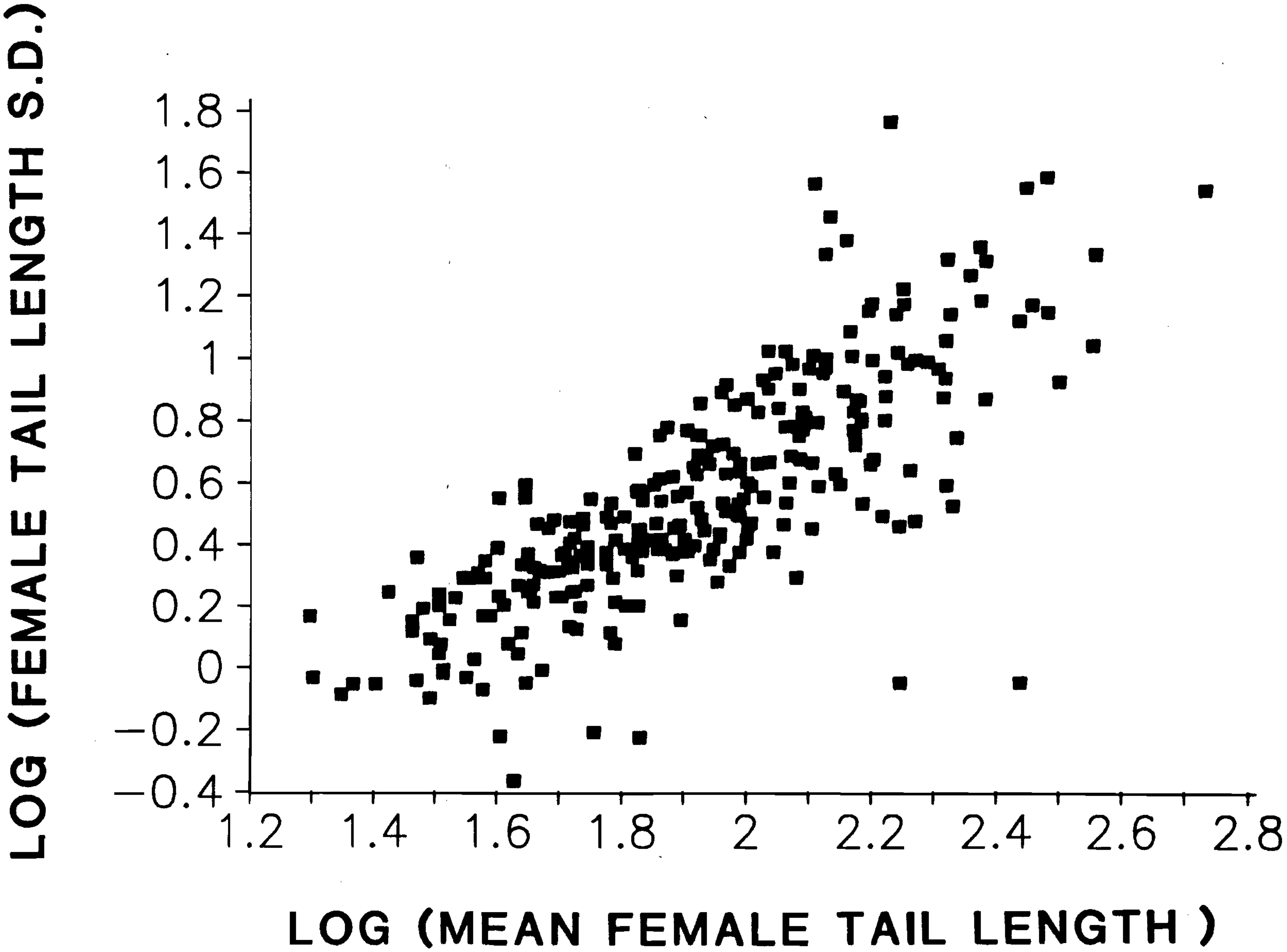

LOG (FEMALE TAIL LENGTH S.D.)
1.8
1.6
1.4
1.2
1
0.8
0.6
0.4
0.2
0
−0.2
−0.4
1.2
1.4
1.6
1.8
2
2.2
2.4
2.6
2.8
LOG (MEAN FEMALE TAIL LENGTH)

FIG.4B

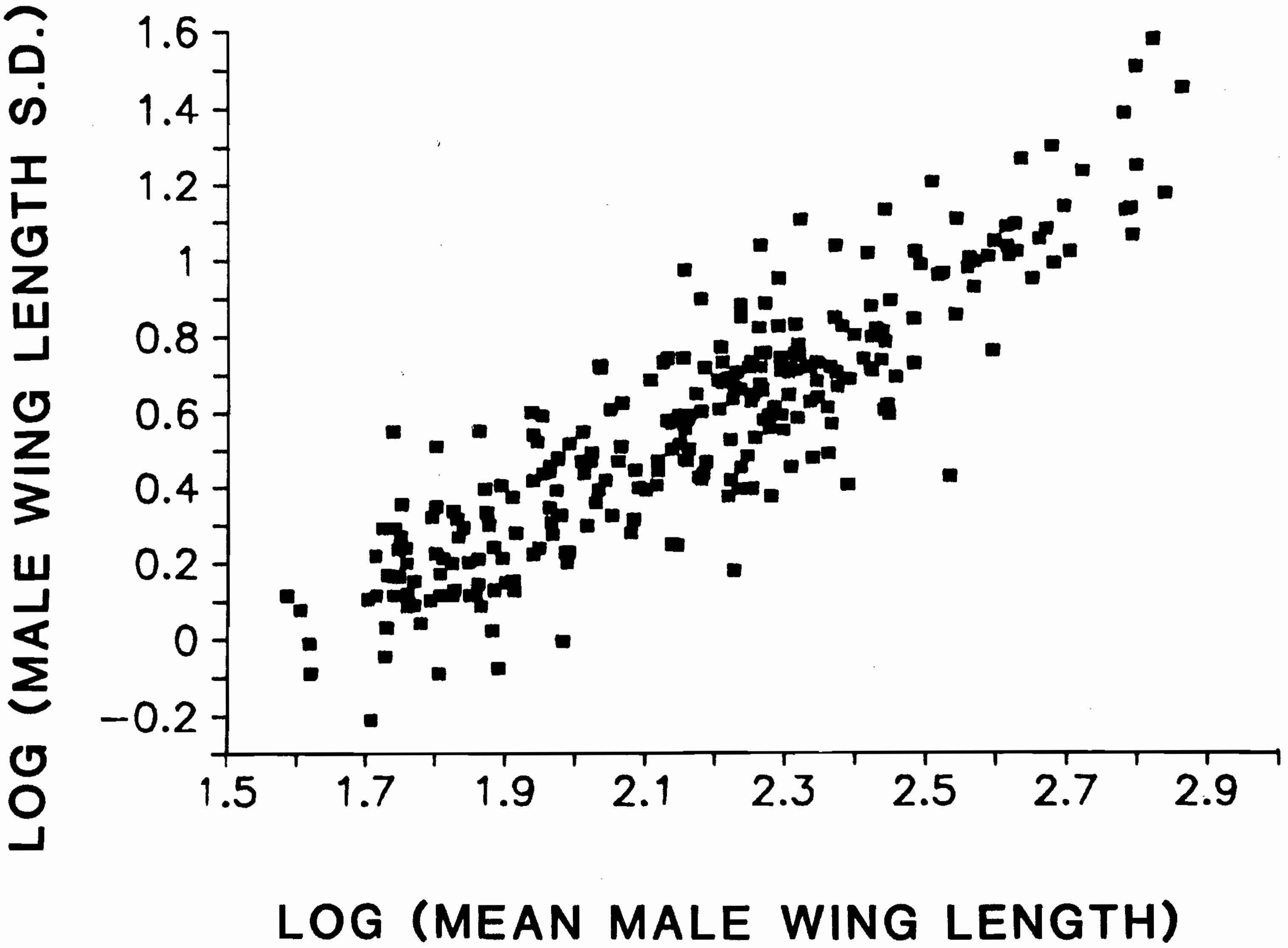

LOG (MALE WING LENGTH S.D.)
1.6
1.4
1.2
1
0.8
0.6
0.4
0.2
0
−0.2
1.5
1.7
1.9
2.1
2.3
2.5
2.7
2.9
LOG (MEAN MALE WING LENGTH)

FIG.4C

FIG.4D

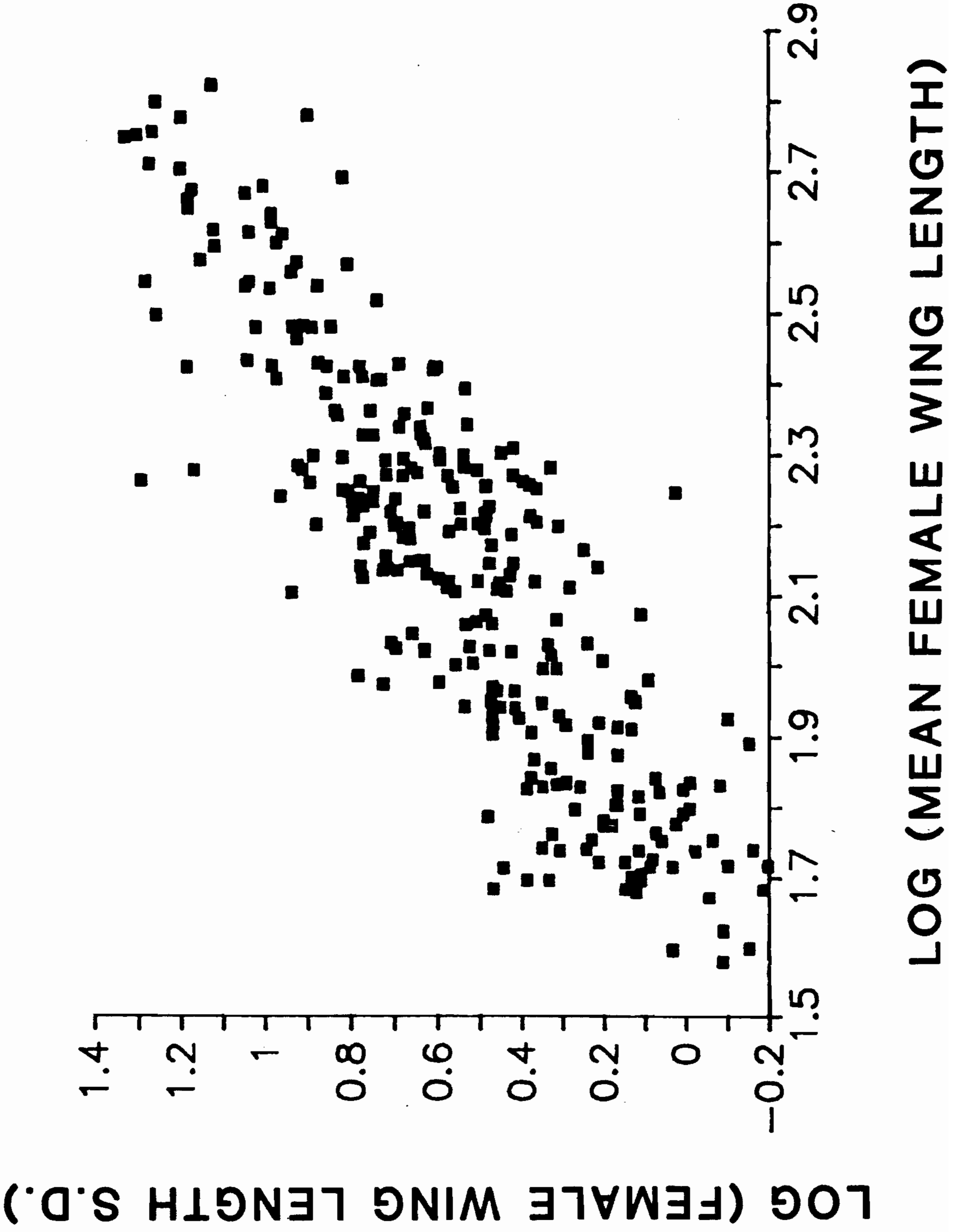

LOG (MEAN FEMALE WING LENGTH)
1.5
1.7
1.9
2.1
2.3
2.5
2.7
2.9
LOG (FEMALE WING LENGTH S.D.)
-0.2
0
0.2
0.4
0.6
0.8
1
1.2
1.4

Figure 5. Relationship between the index of phenotypic variability and the index of sexual size dimorphism for male and female tail length (5a and 5b), and male and female wing length (5c and 5d).

FIG.5B

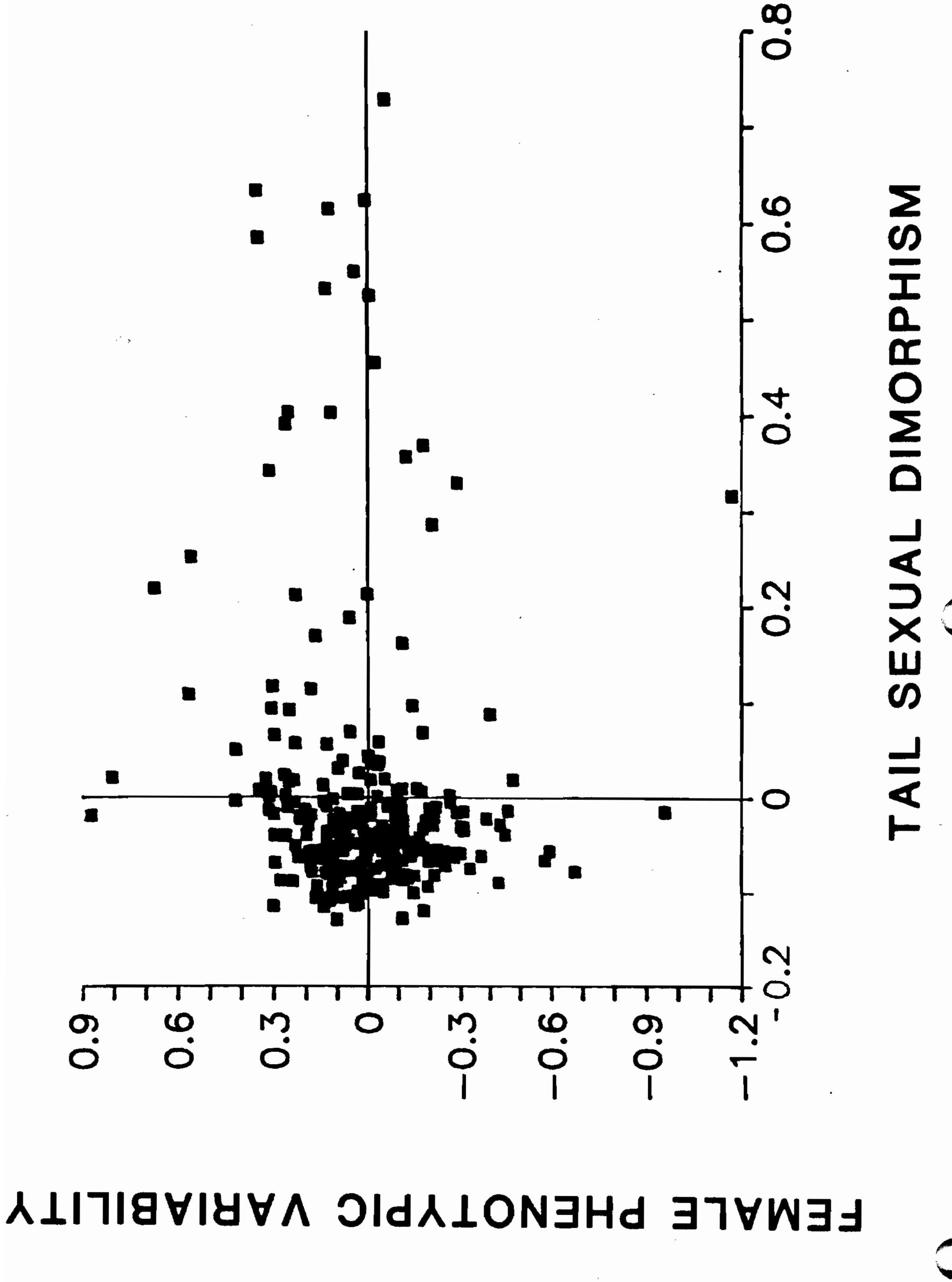

TAIL SEXUAL DIMORPHISM
-0.2
0
0.2
0.4
0.6
0.8
FEMALE PHENOTYPIC VARIABILITY
0.9
0.6
0.3
0
-0.3
-0.6
-0.9
-1.2

FIG.5D

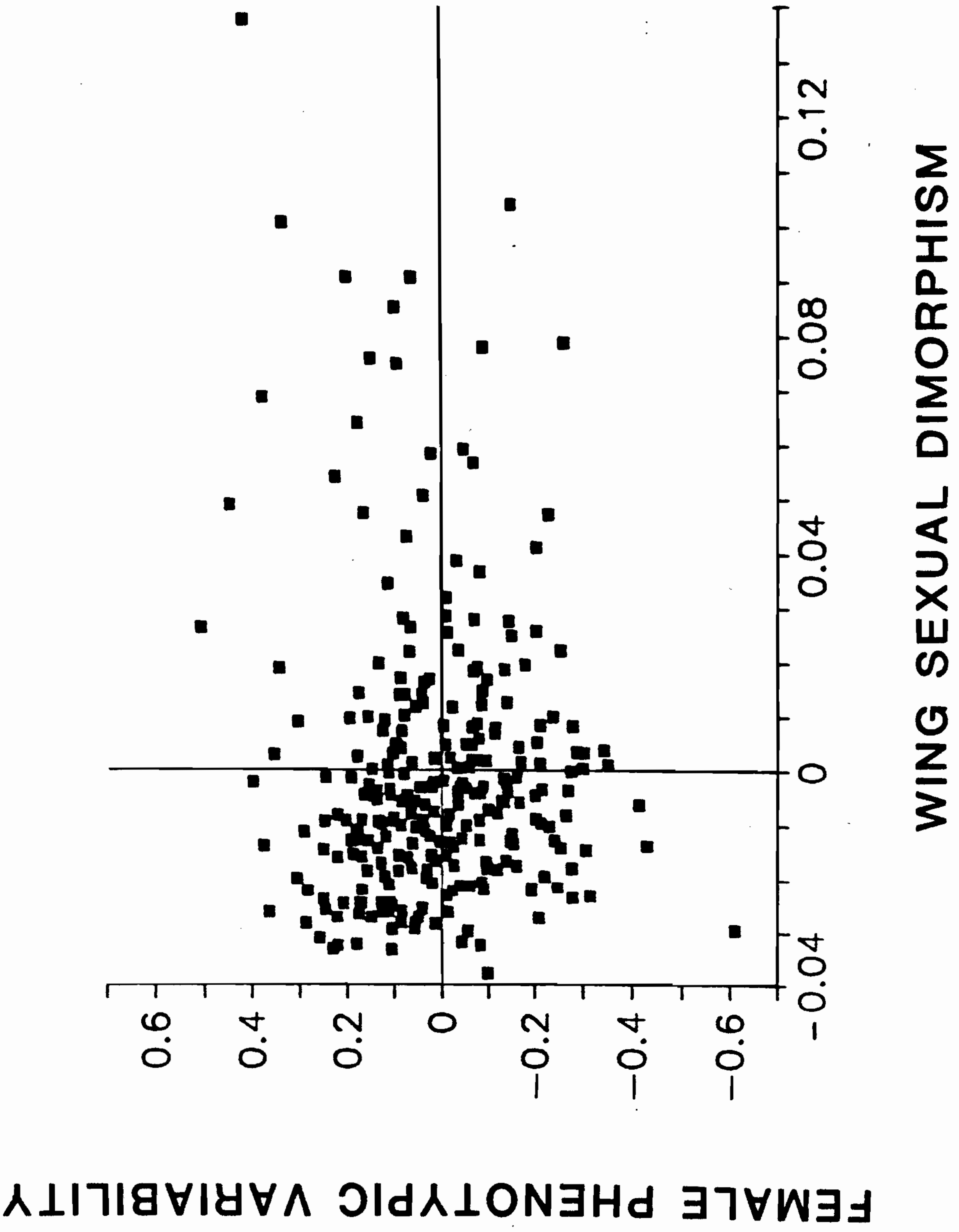

FEMALE PHENOTYPIC VARIABILITY
0.6
0.4
0.2
0
−0.2
−0.4
−0.6
−0.04
0
0.04
0.08
0.12
WING SEXUAL DIMORPHISM

Figure 6. Frequency distribution for male tail length CV (279 species) and male wing length CV (276 species).

FIG.6

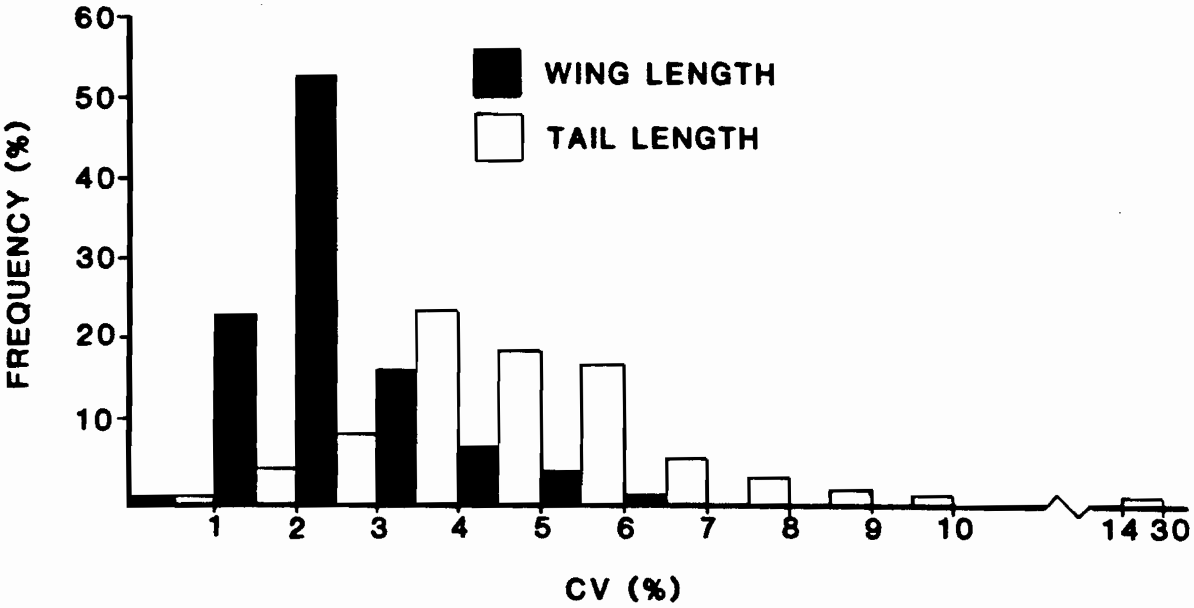
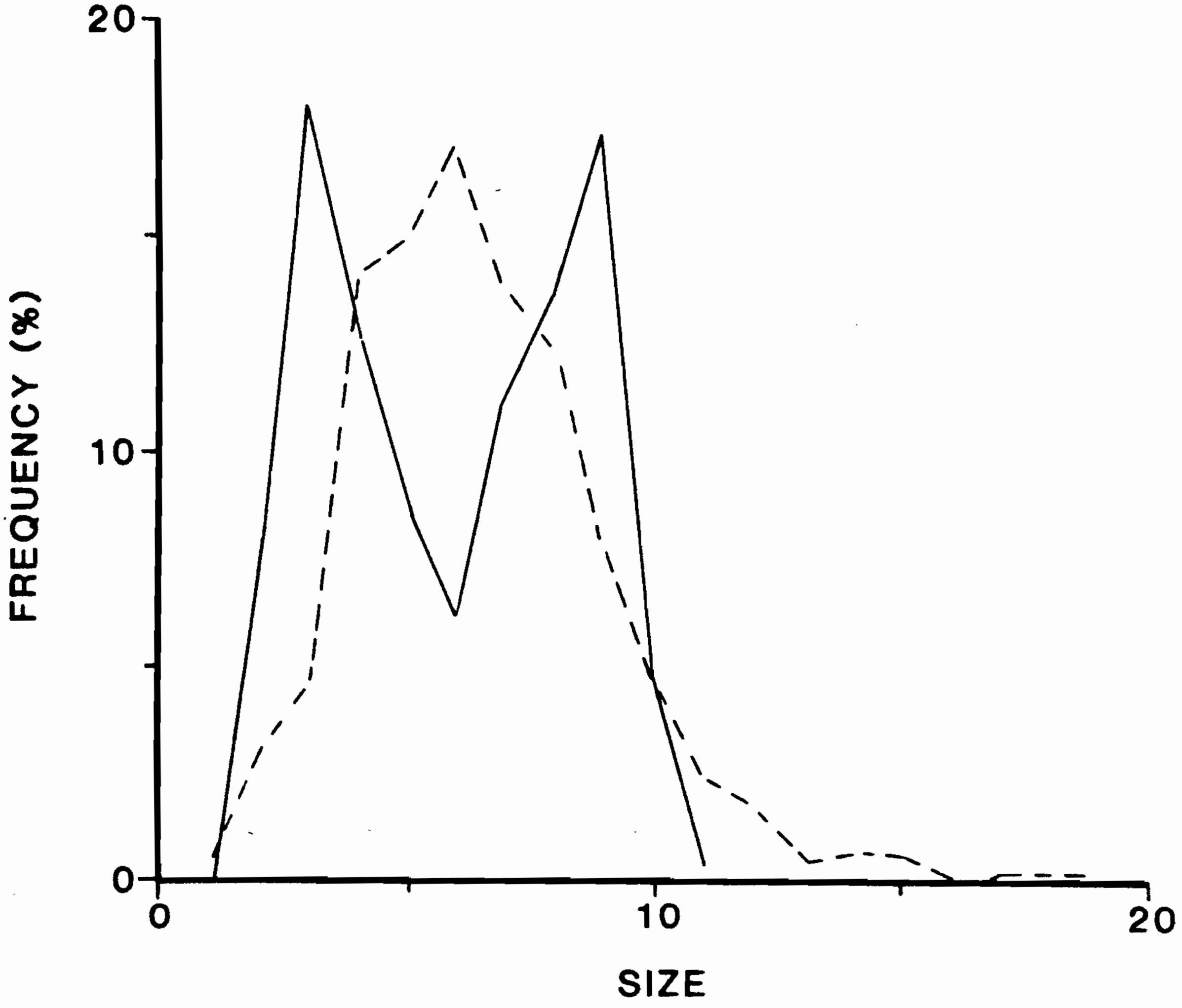

60
50
40
30
20
10
FREQUENCY (%)
WING LENGTH
TAIL LENGTH
1
2
3
4
5
6
7
8
9
10
14
30
CV (%)

Figure 7. Two possible types of frequency distributions of a secondary sexual character with mean = 6.5 and CV = 38%. The bimodal distribution shows the actual distribution of male horn size in the Horned Beetle *Xylotrupes gideon* (Bateson and Brindley 1892). The other distribution is hypothetical.

FIG.7



CHAPTER 4

THE PHENOTYPIC VARIABILITY OF FECUNDITY

ABSTRACT

Three main conclusions emerged from a literature survey of the variability of fecundity in natural populations of herbaceous plants, crustaceans, amphibians, reptiles, birds, and mammals. First, in all these taxonomic groups, with the possible exception of the crustaceans, the Coefficient of Variation (CV = 100* S.D. / Mean) was independent of mean fecundity. Secondly, CV was significantly greater and smaller in plants and birds respectively than in the four other groups. Finally, the variability of fecundity depended on the age at measurement in both birds and plants, with CV increasing systematically from early to later reproductive stages. Thus in birds, CV of fledgling production per nest was three times larger than CV of clutch size at laying; it is suggested that this effect could be explained by the cumulative effect of rather modest levels of stochastic variation in survival rates.

INTRODUCTION

Variation in life history traits (e.g. survival and reproductive rates) and in characters correlated with them (e.g. body size, social dominance, etc.) has always been a central concern of evolutionary biology (Darwin 1885; Bateson 1894; Lewontin 1974). There is, however, no general predictive theory that would tell us how much variation to expect for a certain character in a particular species. Rather, we find a variety of theoretical propositions and empirical observations coming from fields as disparate as theoretical population genetics, quantitative genetics, agricultural and fishery biology, physiology, and ecology. These hypotheses can be organized into two groups depending on whether they favor ultimate (evolutionary) or proximate explanations.

First, evolutionary hypotheses of intra-population variation can themselves be separated into two groups. The first approach stresses the importance of natural selection acting on the genetic component of variation within populations. Its basic tenet is that the genetic variance of a trait should be inversely related to the intensity of selection acting on it. Since traits closely related to fitness are by definition selected most intensely, it is expected that their genetic variation wil be very small. This argument, derived from Fisher's Fundamental Theorem of Natural Selection (Fisher 1958), has since been reformulated and developed as to accomodate various definitions of fitness (e.g. Schmidt and Lawlor 1983). Falconer (1981) collates heritability estimates in a variety of organisms ranging from *Drosophila* to Man supporting the view that genetic variability and the importance of a specific trait to fitness are inversely related. In an extensive review of *Drosophila*, Roff and Mousseau (1987) showed that this generalization held true in a large number of characters, with life history characters showing on average lower heritablity than morphological traits. However, empirical tests of this theory are always weakened to a certain degree by the problem of finding an adequate definition of fitness (Nur 1984) and, as was pointed out by Roff and Mousseau (1987), it explains patterns of genetic variability across classes of characters rather than predict how much variability should be oberved in specific cases.

In the second evolutionary approach to the problem of intra-population variation in life history traits, variability is viewed as a trait itself, a property of the genotype which can be selected (Bradshaw 1965). Caswell (1983) reviews the pertinent literature from this point of view. Specific advantages of phenotypic variability or plasticity have been suggested in a variety of organisms: clutch size and age at maturity in a snail (Brown 1985), egg size in frogs (Crump 1981) and in salamanders (Kaplan 1979), and various life history traits in plants (Lacey et al 1983).

Proximal explanations of phenotypic variability invoke processes such duration of growth and organ complexity (Bradshaw 1965), rate of growth (Atchley 1984), and senescence (David et al 1975). Insofar as size variation has some effect on the amount of variation in life history traits (such as fecundity), models dealing with individual body size variation within populations can also be considered as proximal explanations of life history trait variability. These include stochastic models predicting the variance or the coefficient of variation of size in fish or plant populations (e.g. De Angelis and Coutant 1979), skewness (Yamagishi 1969), and bimodality (Gates 1978) (see also review by Uchmanski 1985).

There is however a large amount of published data concerning the variation of life history characters, in the form of statistics such as the mean and standard deviaton which remains to be summarized. In the present paper, we propose an empirically based predictive theory of phenotypic variability for a particular life history character, fecundity, in a variety of organisms including plants, crustaceans, amphibians, reptiles, birds, and mammals.

METHODS

Data:

Mean and standard deviation (S.D.) for fecundity per female (or were obtained directly from primary or secondary sources , or were calculated from published raw data. Only the mean and S.D. for whole populations were retained; estimates for classes within populations, like size or age classes were excluded. Our study is therefore concerned with estimates of the variation of fecundity at the population level. When more than one record was available for the same species, only the value based on the largest sample size was used. The sampling variance of estimates of mean and S.D. are sensitive to sample size (Sokal and Rohlf 1981), and a sample size of 10 was arbitrarily selected as the cut-off point for inclusion of a case in the present study. The data set included estimates of mean and S.D. for litter size in mammals (27 species), clutch size in birds (79 species), clutch size or brood size in reptiles (70 species), amphibians (25 species) and crustaceans (36 species), and fruit number in herbaceous plants (94 species). The data and sources are listed in Table 1.

Analysis:

This section deals with some problems in the measurement of phenotypic variability. Variance or S.D. are standard measurements of variability or dispersion. However, when characters with different means are compared, it is a common observation that S.D. and the mean are positively correlated. There is therefore a need to take this effect into account in order to have an index of variability independent of the mean. The Coefficient of Variation (CV = 100*S.D./mean) is usually selected for this purpose (Yablokov 1974; Van Valen 1980). However, Yablokov (1974), in an extensive review of the phenotypic variability in mammals, has show that, despite positive relationships between S.D. and the mean, CV tends to vary inversely with size (mean) when morphometric characters of different magnitudes are compared within species. Lande (1977) has since provided a theoretical explanation, based on the non-additivity of CVs, for this empirical finding. His explanation is probably difficult to apply to interspecific comparisons of fecundity variability; nevertheless, the possibility of mean-related effects on fecundity variability remains to be empirically investigated. In the present paper, the following statistical procedure was used to achieve this goal. The relationship between S.D. and mean can be described by the following general equation:

$$\text{S.D.} = b^{*}\text{Mean}^{a} \qquad (1)$$

With a = 1, CV (S.D./mean) is independent of the mean, and is simply proportional to the value of b. If a<1, then C.V. will decrease as the mean increases, as was observed in Yablokov's (1974) data on morphometric variability in mammals. Conversely, a>1 would indicate that CV increases with the mean and species with high mean fecundity would also be more variable. The linear logarithmic form of equation (1) is usually used for least-squares regression analysis:

$$\log_{10}\text{S.D.} = a^{*} \log_{10} \text{mean} + \log_{10} b \qquad (2)$$

A statistical justification of regressing log S.D. on log mean instead of simply S.D. on mean is that sampling variance of S.D. is proportional to S.D. itself (Sokal and Rohlf 1981): therefore a plot of S.D. vs mean would be expected to show heteroscadisticity for the dependent variable, S.D., a condition undesirable in regression analysis (Sokal and Rohlf 1981). This regression model serves two purposes:

1- To test if S.D. and mean are positively correlated and that therefore variability is to be measured in relative terms (CV). This is achieved by testing the significance of the departure of "a" from the value of 0 with a standard t-test (Sokal and Rohlf 1981).

2- To test for the independence of CV from the mean. This is achieved by testing the significance of the departure of "a" from the value of 1 with a t-test (a-1/s.e. of slope).

RESULTS

Scaling of Variability

Significant positive relationships between log S.D. and log mean fecundity were found in all six taxonomic groups (Table 2 and Figure 1 to 5). Visual inspection of the residual plots as a function of the independent variable, log mean, showed that, with the possible exception of the bird data, the double logarithmic regression model provided an adequate description of the relationship between S.D. and mean. For birds, residual values were not uniformly distributed over the range of mean clutch sizes (Figure 5), with exceptionally large negative residual values around means of 2, 3, and 4. These refer mainly to species of Charadriidae that have highly determinate clutch size.

The slope of the relationships between log S.D. and log mean ("a") did not significantly differ from the value of 1 (Table 2) except for crustaceans. Therefore , relative variability , measured by CV, is independent of mean fecundity in plants, amphibians, reptiles, birds, and mammals. In crustaceans, the slope (0.66) was significantly smaller than 1, showing that brood size CV tends to be smaller for species with large fecundity. However, it should be noted that, with one exception, all these data were obtained from only two taxonomic families (Cumaceae and Mysidaceae) and this result should be accepted with caution.

Taxonomic Comparisons of Variability:

Figure 6 shows the relative positions of the predicted log S.D. - log mean relationships for the six taxonomic groups. Differences in the elevation of the regression lines suggest that variation increases from birds, through mammals, crustaceans, amphibians and reptiles, to plants. Analysis of variance showed that plants and birds, which had the highest and lowest mean CVs respectively, differed significantly from the rest (Table 3). No significant differences in CV were detected among crustaceans, reptiles, amphibians, and mammals. As noted earlier, CV of fecundity in crustaceans was not independent of the mean. Exclusion of this group from the analysis of variance did not however change our results in any significant way. The frequency distribution histograms of CV in each taxonomic group (Figure 7a-f) illustrate these conclusions, and also shows that fecundity CV varies substantially between species within each taxonomic group. This variation is greatest among plants, where CV of number of fruits per plant ranged from 10% to more than 240% (Figure 7a). Thus the variability of this component of individual fecundity is not only greater than in the five other animal groups, but it is also very variable itself. It would therefore not be possible to anticipate the degree of variability to expect for this character in a particular field study unless some correlate of CV can be identified. In birds, CV never exceeded 40% (Figure 7f), with the majority of species clustering between the values of 10 and 30%.

Propagation of Variability

In all bird species included in the present study, CV of the number of young fledged per nest (CV_f) exceeded the CV of clutch size at laying (CV_c) (Table 4). For the data based on all nests, the mean difference CV_f-CV_c was 41.4 (s.e. = 7.22), and significantly exceeded the value of 0 ($p<0.001$). The increase in CV from the clutch to the fledging stage was smaller (25.8; s.e. = 9.63), though still significant ($p < 0.02$), when the calculation was based on successful nests (nests producing at least one fledgling). Thus, large increases in CV from laying to fledging stage were usually accompanied by a higher mortality rate (e.g. *Corvus corax, Pica pica*), leading to greater frequencies of total nest failure, while species with lower mortality rates (e.g. *Anser caerulescens, Delichon urbica*) exhibited more modest increases in CV. A similar increase in variability through successive reproductive stages was observed in plants (Table 5). Here the initial stage (Trait 1) was the number of buds, flowers, or incipient fruits per plant, and the subsequent stage (Trait 2) corresponded to the number of seeds or mature fruits per plant. With only one (border line) exception (*Ludwigia leptocarpa*), CV always increased from Trait 1 to Trait 2. Over 11 cases, which included 9 species, the average increase in CV (CV_2-CV_1) was significant (mean = 17.3; s.e. = 3.67; $p < 0.001$). Hence both the plant and the bird data showed that the variability of reproductive output among individuals increased from earlier to later stages of reproduction.

DISCUSSION

The main results of the present study can be summarized as follows. First, the phenotypic variability of fecundity in organisms including herbaceous plants, amphibians, reptiles, crustaceans, birds, and mammals is described in terms of CVs. Within these taxonomic groups, this index of variability is independent of mean fecundity. Only among crustaceans did CV tend to decrease with the mean; however, the generality of this result is questionable since, with one exception, all the data came from only two taxonomic families.

Secondly, significant statistical differences in CV were found among the same six taxonomic groups. Plant exhibited the highest level of intrapopulation variability in fecundity, followed, by amphibians, reptiles, crustaceans, and mammals. No significant differences in CV were found between these last four groups. Birds showed less variability in fecundity and average clutch size CV was significantly smaller than in the other five groups.

Thirdly, we found that the amount of phenotypic variability observed in a particular species depends on the particular reproductive stage considered. In birds, the CV of the number of young fledged per nest always exceeded that of clutch size at the time of laying, and in plants there was a similar increase in variability from earlier to later stages of reproduction.

Scaling of Phenotypic Variability in Fecundity

The scaling of phenotypic variablity is at the heart of some recent theoretical and empirical work in population biology. Lacey et al (1983) have suggested that, depending on the concavity of the relationship between a fitness measurement and a correlated character, high variance in this character can lead to a decrease or increase in expected fitness. Different combinations of variances and means can therefore lead to the same expected fitness. Similar trade-offs are expected when fitness itself varies in time, when the geometric rather the arithmetic mean of fitness is usually accepted as the best measure of expected long-term fitness (Gillespie 1977; Goodman 1984). Temporal variance in fitness will reduce expected fitness, since the geometric mean decreases as the variance increases; given a certain arithmetic mean fitness, therefore, an increase in CV will lead to a decrease in geometric mean fitness. Again different combinations of mean and CV can lead to the same geometric fitness. Assuming that spatial variability is somehow related to temporal variability, Ritland and Jain (1984) interpreted positive correlations between CV and mean for various life history characters across species and populations of annual plants as evidence of such trade-offs between high arithmetic fitness and temporal variability. We found that in herbaceous plants, reptiles, amphibians, mammals, and birds, CV was independent from arithmetic mean fecundity. Our study therefore provides no evidence for a relationship between reproductive output and its variability. However, we do not assert that all hypotheses which predict a negative correlation between the mean and CV of fitness components have been decisively falsified. In the first place, our bivariate log S.D. - log mean relationships include many species that are not closely related, and it could be argued that positive trends between CV and mean fecundity should be expected only when closely related species, or even populations of the same species, are compared. Secondly, and more importantly, reproduction and survival will vary with age in most of the species discussed here. Under these conditions, the mean and the CV of fecundity for the whole population cannot be equated with the mean and the CV of fitness.

However, estimates of mean and CV of fecundity based on pooled age classes are of theoretical and empirical importance to another field of evolutionary biology, the quantitative study of the intensity of natural and sexual selection, Crow's (1958) index of total opportunity for natural (or sexual) selection ("I") has been used in a number of life history studies (e.g. Wade and Arbold 1980; Kluge 1981; Clutton-Brock 1983). "I" is defined as:

$$I = \mathrm{Var}/\mathrm{mean}^2 = \mathrm{S.D.}^2/\ \mathrm{mean}^2 = \mathrm{CV}^2$$

Assuming the character to be a component of fitness, such as fecundity, this index measures the maximum shift in mean fitness that would occur in one generation, given that all the observed variability is genetic in origin (Wade and Arnold 1980). Since this index is equal to the square of CV, our conclusions concerning the scaling of CV can be expressed in terms of "I", or total opportunity fo the action of selection. Thus, like CV, "I" is independent of the mean in five of the six taxonomic groups included in the present study (the crustaceans being the possible exception). For example, the intensity of natural selection resulting from variation in female fecundity (I_f, Wade and Arnold 1980) in amphibians with relatively small clutch size, such as the frog *Rana tagoi* (mean number of eggs per female = 104.7, $I_f = 0.078$, Kuramoto 1978), does not differ substantially from that of a highly fecund species such as *Bufo regularis* (mean fecundity = 10055, $I_f = 0.082$, Barbault 1984).

Recently, several workers (e.g Fincke 1982; Clutton-Brock 1983; Harfernick and Brown 1986) have favored the use of "I" calculated from lifetime reproductive success rather than from cross-sectional measurements made over a period of time shorter than lifespan, as is the case here (but see Kluge 1981; Price 1984; Schluter and Smith 1986 for cross-sectional estimates of "I"). As pointed out by Fincke (1986), the two methods may not yield equivalent results, and "I" values based on cross-sectional data probably overestimate the selection intensity acting through variation in lifetime female fecundity. However, such estimates of I_f, based on the pooling of all female age classes, are probably more relevant to the measurement of the selection intensity acting on males (I_m, Wade and Arnold 1980) than those based on lifetime reproductive success. Consider a species in which males may mate with females of any age. This situation is likely to be common in most animal taxa. If mating success (lifetime or otherwise) is exactly the same for all males, the minimum value for I_m is equivalent to I_f (assuming a sex-ratio of 1), that is, variance in reproductive success among males is solely a function of variance in fecundity among females. Using I_f based on lifetime female fecundity as an estimate of this minimum value of I_m would obviously be misleading since males are free to mate with females of different age and fecundity. In other words, variance in lifetime female reproductive success could be zero, all females going through exactly the same age-related changes in fecundity, yet high variance in male reproductive success could still exist, given that males mate with females of different ages and reproductive potentials. Hence a value of I_f based on all female age classes combined, as presented here, represents a better index of the variability in female quality experienced by males than I_f based on female lifetime fecundity. Thus, for example, in some reptiles and amphibians, CV of female fecundity reached values near 100% (Table 3), which represents an I_f (and an estimate of minimum I_m) value of 1.

Taxonomic Comparisons of Variability in Fecundity

We found large differences in CV both within and between major taxonomic groups. There are two explanations that could possibly account for differences among groups. For example, plant fecundity may be more variable than clutch size in birds because a character correlated with fecundity, perhaps size, is more variable in plants than in bird. An alternative explanation could be that in these two groups size is equally variable, and that it is rather the relationship between fecundity and size that differs and causes the difference in fecundity variability. These two mechanisms are naturally not mutually exclusive, and their relative importance remains to be investigated. An example of the second type of control of variability of fecundity would be the existence of size thresholds for reproduction in plants (e.g. Werner and Caswell 1977; Baskin and Baskin 1979). In semelparous organisms with constrained lifespans, such as in annual plants, such thresholds should not exist since the benefit of not reproducing at the end of the first season (increased survival or fecundity in the next season) are by definition nil (Bell 1980). In the next chapter, we test the hypothesis that the variability of fecundity is higher in annual than in perennial plants.

Apart from these interpretations of patterns in phenotypic variability, our results can be usefully applied in evolutionary studies. Log S.D.- log mean relationships can be viewed as null hypotheses in interspecific comparisons of variability. First, they indicate whether CV varies with the mean, and therefore whether a correction for the mean should be made when comparing the CVs of species with different means. Secondly, the distributions of CVs within different taxonomic groups, as in Figure 6, provide some indication about what to expect when a new species is studied. For example, a bird species with clutch size CV of 40% would be considered very variable, while an equivalent CV observed in a plant species would be well below the norm for that group. Log S.D.- log mean relationships can also be used in designing sampling procedures. Given an approximate estimate of mean fecundity, S.D. can be estimated and the sample size required to obtain specific confidence interval around the mean can thus be selected.

Propagation of Variability

Finally, we found that phenotypic variability in fecundity increases from early to later reproductive stages. A simple explanation for this increase in variability with age could be the cumulation of random environmental variation in survival rates between early and later stages. A simple model, in which survival rate varies independently of initial clutch size, is able to explain the increase in CV observed in the bird and plant data. Consider the simple two-stage life history:

$$N(\text{fledged}) = N(\text{initial clutch size}) * (\text{survival rate})$$

Both clutch size at laying and subsequent survival rate will have a mean and a variance associated with them and therefore CVs : CV_c and CV_s respectively. Assuming clutch size and survival to be independent of each other, the CV of the number of fledglings (CV_f) can be exactly calculated as:

$$(CV_f)^2 = (CV_c * CV_s)^2 + (CV_c)^2 + (CV_s)^2 \qquad \text{(Colquhoun 1970)}$$

For the avian data based on all nests (Table 4) we found a mean CV_f of 60.8% and a mean CV_c of 19.4%, Solving the above equation we find that CV_s = 3.0%. Thus, assuming independence between survival rate and clutch size, a rather modest amount of random variation in survival rate can triple the amount of variability found in initial clutch size. Note that this result is independent of initial mean clutch size, and random survival rate is thus expected to have the same impact on the variability of a clutch size with a mean of 1000 than on one with a mean of 4. Our results suggest the existence of a general pattern in which the phenotypic variability of fitness characters, or at least those related to offspring production, steadily increases with time. It would be interesting to determine whether heritability also decreases with time, as our random survival model implies, remains approximately constant, or increases, in which case genetic variation would also increases with age, paralleling the increase in non-genetic variation. Another possible explanation for the increase in CV with time, at least for birds, might be that fledgling production is more affected by female age and experience than initial clutch size is, and that the increase in CV of fledgling number per nest is a reflection of this.

LITERATURE CITED

Aker, C.L. 1982. Regulation of flower, fruit and seed production by a monocarpic perennial, *Yucca whipplei*. J. Ecol. 70: 357-372.

Alatalo, R.V., and A. Lundberg. 1984. Density-dependence in breeding success of the Pied Flycatcher (*Ficedula hypoleuca*). J. Anim. Ecol. 53: 969-977.

Allen, S.H. 1984. Some aspects of reproductive performance in female Red Fox in North Dakota. J. Mammal. 65: 246-255.

Atchley, W.R. 1984. Ontogeny, timing of development, and genetic variance-covariance structure. Amer. Nat. 123: 519-540.

Ballinger, R.E. 1974. Reproduction of the Texas Horned Lizard, *Phrynosoma cornutum*. Herpet. 30: 321-327.

Barbault, R. 1984. Stratégies de reproductions de quelques amphibiens anoures tropicaux. Oikos 43: 77-87.

Baskin, J.M., and C.M. Baskin. 1979. Studies on the autecology and population biology of the weedy monocarpic perennial, *Pastinaca sativa* . J. Ecol. 67: 601-610.

Bateson, W. 1894. Materials for the Study of Variation. London.

Bell, G. 1980. The costs of reproduction and their consequences. Amer. Nat. 116: 45-76.

Berdnarz, J.C. 1987. Successive nesting and automnal breeding in Harris' Hawks. Auk 104: 85-96.

Bergier, P., and O. Badau. 1979. Compléments sur la reproduction du grand-duc *Bubo bubo* en Provence. Alauda 47: 271-275.

Birkhead, M., Bacon, P.J., and P. Walter. 1983. Factors affecting the breeding success of the Mute Swan *Cygnus olor* . J. Anim. Ecol. 52: 727-741.

Blondel, J. 1985. Breeding strategies of the Blue Tit and Coal Tit (*Parus*) in mainland and island mediterannean habitats: A comparison. J. Anim. Ecol. 531-556.

Bradshaw, A.D. 1965. Evolutionary significance of phenotypic plasticity in plants. Adv. Genet. 13: 115-155.

Brown, A.D. 1985. Mechanisms of life history adaptation in temporary pond snail *Lymnaea elodes* (Say.). Amer. Malac. Bull. 3: 143-150.

Bruce, R.C. 1972. Variation in the life cycle of the salamander *Grynophilus porphyritus* . Herpet. 28: 230-245.

Bryant, D.M. 1979. Reproductive costs in the House Martin (*Delichon urbica*). J. Anim. Ecol. 48: 655-675.

Bunn, D.S., Warburton, A.B., and R.D.S. Wilson. 1970. The Barn Owl. Payser, T. and A.D. (eds.). England.

Burger, A.E, 1979. Breeding biology, moult and survival of Lesser Sheathbills *Chionis minor* at Marion Island. Ardea 67: 1-14.

Caswell, H. 1983. Phenotypic plasticity in life-history traits: Demographic effects and evolutionary consequences. Amer. Zool. 23: 35-56.

Christy, E.J., and R.R. Sharitz. 1980. Characteristics of three populations of a swamp annuals under different temperature regimes. Ecology 61: 454-460.

Congdon, J.D., and D.W. Tinkle. 1982. Reproductive energetics of the Painted Turtle (*Chrysemis picta*). Herpet. 38: 228-237.

Corey, S. 1981. Comparative fecundity and reproductive strategies in seventeen species of Cumacea (Crustacea: Peracarida). Mar. Biol. 62: 65-72.

Cramp, J. 1977. The Handbook of the Birds of Europe, the Middle East, and North Africa. Oxford University Press, Oxford.

Crow, J.F. 1958. Some possibilities of measuring selection intensities in man. Human Biol. 10: 1-13.

Crump, M.L. 1981. Variation in propagule size as a function of environmental uncertainty for Tree Frogs. Amer. Nat. 117: 724-727.

Darwin, C.R. 1885. Variation under Domestication. John Murray, London.

David, J., Cohet, Y., and P. Fouillet. 1975 The variability between individuals as a measure of senescence: A study of the number of eggs laid and the percentage of hatched eggs in the case of *Drosophila melanogaster*. Exp. Geront. 10: 17-25.

DeAngelis, D.L., and C.C. Coutant. 1979. Growth rates and size distributions of first-year Smallmouth Bass populations: Some conclusions and a model. Trans. Amer. Fish. Soc. 108: 137-141.

Dunham, A.E. 1972. Demogaphic and life-history variation among populations of iguanid lizards *Urosaurus ornatus* : Implications for the study of life-history phenomena in lizards. Herpet. 36: 99-104.

Edwards, J. 1985. Effects of herbivory , distribution, and status of

Pacifasciacus fortis (Decapoda: Astacidae). Calif. Fish. and Game 68: 197-212.

Falconer, D.S. 1981. Introduction to Quantitative Genetics. 2nd edition. Longham Group Ltd., London.

Fincke, O.M. 1982. Lifetime mating success in a natural population of the damselfly *Enallagma hageni* (Walsh) (Odonata: Coenagrionidae). Behav. Ecol. Sociobiol. 10: 293-302.

Fincke, O.M. 1986. Lifetime reproductive success and the opportunity for selection in a nonterritorial damselfly (Odonata: Coenagrionidae). Ecol. 40: 791-803.

Finney, G., and F. Cooke. 1978. Reproductive habits in the Snow Goose: The influence of female age. Condor 80: 147-158.

Fisher, R.A. 1958. The Genetical Theory of Natural Selection. Dover, New York.

Fitch, H.S. 1954. Life history and ecology of the Five-lined Skink, *Eumeces fasciatus* . Univ. Kansas Mus. Nat. Hist. 8: 1-156.

Fitch, H.S. 1970. Reproductive cycles of lizards and snakes. Univ. Kansas Mus. Nat. Hist. Misc. Publ. 52: 1-247.

Fitch, H.S. 1975. A demographic study of the Ringneck Snake (*Diadophis punctatus*) in Kansas. Univ. Kansas Mus. Nat. Hist. Misc. Publ. 62.

Fleming, T.H. 1971. Population ecology of three species of neotropical rodents. Misc. Publ. Mus. Zool. Univ. Mich. 143: 1-77.

Foote, R.W. 1978. Nesting of *Podocnemis unifilis* (Testudines: Pelomedusinae) in the Colombian Amazon. Herpet. 34: 333-339.

Frazer, N.B., and J.I. Richardsson. 1985. Annual variation in clutch size and frequency for Loggerhead Turtles, *Caretta caretta* , nesting at Little Cumberland Island, Georgia, USA. Herpet. 41: 246-251.

Gates, D.J. 1978. Bimodality in even-aged plant monocultures. J. Theor. Biol. 71: 525-540.

Gibbons, J.W. 1972. Reproduction, growth, and sexual dimorphism in the Canebrake Rattlesnake (*Crotalus horridus atricaudulatus).* Copeia 1972: 222-226.

Gill, B.J. 1982. Breeding in the Grey Warbler *Gerygone igata* at Kaikowa, New Zealand. Ibis 124: 123-147.

Gillespie, J.H. 1977. Natural selection for variance in offspring number: A new evolutionary principle. Amer. Nat. 111: 1010-1014.

Glazier, D.S. 1985. Energetics of litter size in five species of *Peromyscus* with generalizations for other mammals. J. Mammal. 66: 629-642.

Goodman, D. 1984. Risk spreading as an adaptive strategy in iteroparous life histories. Theor. Pop. Biol. 25: 1-20.

Goodwin, T.M., and W.R. Marion. 1978. Aspects of the nesting ecology of American Alligators (*Alligator mississipiensis*) in North-Central Florida. Herpet. 34: 33-39.

Hafernick, J.E. Jr., and R.W. Garrisson. 1986. Mating success and survival rate in a population of damselflies: Results at variance with theory ? Amer. Nat. 128: 353-365.

Hannon, S.J., and J.N.M. Smith. 1984. Factors influencing are-related reproductive success in the Willow Ptarmigan. Auk 101: 848-854.

Harris, S. 1979. Age-related fertility and productivity in Red Foxes, *Vulpes vulpes* , in suburban London. J. Zool. 187: 195-199.

Hasegawa, M. 1984. Biennial reproduction in the lizard *Eumeces okadae* on Miyake-Kima, Japan. Herpet. 40: 194-199.

Hasler, M.J., Hasler, J.F., and A.V. Nalbandof. 1977. Comparative biology of Musk Shrews (*Suncus marinus*) from Guam and Madagascar. J. Mammal. 58: 285-290.

Hooper, E.T., and M.D. Carleton. 1976. Reproduction, growth and development in two contiguously allopatric rodent species, Genus Scotinomys. Misc. Publ. Mus. Zool. Univ. Mich. 151: 1-52.

Innes, D.G., and J.S. Millar. 1981. Body weight, litter size, and energetics of reproduction in *Cleithrionomys gapperi* and *Microtus pennsylvaticus* . Can. J. Zool. 59: 785-789.

Iverson, J.B. 1977. Reproduction in freshwater and terrestrial turtles in North Florida. Herpet. 33: 205-212.

Iverson, J.B. 1978. Reproductive cycle of female Loggerhead Musk Turtles (*Sternotherus minor minor*) in Florida. Herpet. 34: 33-39.

Jain, A.P. 1984. Relationship between body weight of mother and size of litter in Antelope Rat, *Tatera i. indica* Hardwicke. Mammalia 48: 143-148.

Jarvinen, A. 1982. Ecology of the Siberian Tit *Parus cinctus* in NW Finnish Lapland. Ornis. Scand. 13: 47-55.

Jemiolo, B. 1983. Reproduction in a laboratory colony of the female Pine Vole, *Pitmys subterraneus* . Acta Therio. 28: 197-207.

Jurik, T.W. 1985. Differential costs of sexual and vegetative reproduction in wild Strawberry populations. Oecologia 66: 394-403.

Kaplan, R.H. 1979. The implications of ovum size variability for offspring fitness and clutch size within several populations of salamanders (*Ambystoma*) Evolution 34: 51-64.

Kluge, A.G. 1981. The life history, social organization, and parental behavior of *Hyla rosenbergi,* a nest-building gladiator frog. Misc. Publ. Mus. Zool. Univ. Mich. 160.

Kristiansson, H. 1981. Young production of European Hedgehog in Sweden and Britain. Acta Therio. 26: 504-507.

Kuramoto, N. 1978. Correlations of quantitative characters of fecundity in amphibians. Evolution 32: 287-296.

Lacey, E.P., Real, L., Antonovics, J., and D.G. Heckel. 1983. Variance models in the study of life histories. Amer. Nat. 122: 114-131.

Lackey, J.A. 1978. Reproduction, growth, and development in high-altitude and low-altitude populations of *Peromyscus leucopus* (Rodentia). J. Mammal. 59: 69-83.

Lande, R. 1977. On comparing coefficient of variation. Syst. Zool. 26: 214-217.

Landers, J.L., Garner, J.A., and W.A. Mc Rae. 1980. Reproduction of Gopher Tortoises (*Gopherus polyphemus*) in Southwestern Georgia. Herpet. 36: 353-361.

Legay, J.M., and D. Pontier. 1985. Relation âge-fécondité dans les populations de chats domestiques, *Felix catus* . Mammalia 49: 395-406.

Lewontin, R.C. 1974. The Genetic Basis of Evolutionary Change. Columbia University Press, New York.

Leverich, W.J., and P.A. Levin. 1979. Age-specific survivorship and reproduction in *Phlox drummondii* . Amer. Nat. 113: 881-903.

Lundberg, A. 1981. Population ecology of the Ural Owl *Stryx uralensis* in Central Sweden. Ornis Scand. 12: 111-119.

Mauchline, J. 1973. The broods of the British Mysidacea (Crustacea). J. Mar. Biol. Ass. UK. 53: 801-817.

Michalak, I. 1983. Reproduction, maternal and social behaviour of the European Water Shrub under laboratory conditions. Acta Therio. Suppl. 1: 3-24.

Murphy, E.C. 1978. Breeding biology of House Sparrows: Spatial variation. Condor 80: 180-193.

Neal, E.G. 1977. Badgers. Blanfad Press, Poole, Dorset, UK.

Newton, I., and M. Marquiss.1984. Seasonal trend in the breeding performance of Sparrowhawks. J. Anim. Ecol. 53: 809-829.

Nolan, V. Jr. 1978. The ecology and behavior of the Prairie Warbler *Dendroica discolor* . Ornit. Monogr. 26: 1-551.

Nur, N. 1984. Fitness, population growth and natural selection. Oikos 44: 413-414.

Okada, Y. 1966. Fauna Japonica. Anura (Amphibia). Biogeographical Society of Japan (ed.), Tokyo, Japan.

Parker, W.S. 1973. Notes on the reproduction of some lizards from Arizona, New Mexico, and Utah. Herpet. 29: 258-264.

Petranka, J.W. 1984. Breeding migrations, breeding season, clutch size, and oviposition of Stream-breeding *Ambystoma texanum* . J. Herpet. 18: 106-112.

Petrinovich, L., and T.L. Pattersson. 1983. The White-crowned Sparrow: Reproductive success (1975-1980). Auk 100: 811-825.

Pettus, D., and G.M. Angleton. 1967. Comparative biology of montane and piedmont Chorus Frogs. Evolution 21: 500-507.

Pfeifer, S.R. 1982. Variability in reproductive output and success in *Spermophilus elegans* Ground Squirrels. J. Mammal. 63: 282-289.

Pianka, E.R. 1971. Ecology of the Agamid lizard *Amphibolurus isolepis* in Western Australia. Copeia 1971: 527-536.

Pietiainen, H., Saurola, P., and V.A. Varsanen. 1986. Parental investment in clutch size and egg size in the Ural Owl *Strix uralensis* . Ornis Scand. 17: 309-325.

Powell, R.A. 1982. The Fisher. Life History, Ecology, and Behavior. University of Minnesota Press, Minneapolis.

Price, T.D. 1984. Sexual selection on body size, territory and plumage variables in a population of Darwin's finches. Evolution 38: 327-341.

Primack, R.B. 1980. Variation in the phenology of natural populations of montane shrubs in New Zealand. J. Ecol. 68: 849-862.

Reese, K.P., and J.A. Kadlec. 1985. Influence of high density and apparent age on the habitat selection and reproduction of Black-billed Magpies. Condor 87: 96-105.

Ritland, K., and S. Jain. 1984. The comparative life histories of two annual *Limnanthes* species in a temporarily variable environment. Amer. Nat. 124: 656-677.

Roberts, M., Maliniak, E., and M. Deal. 1984. The reproductive biology of the Rock Cavy, *Kerodon rupestris* , in captivity. A study of reproductive adaptation in a trophic specialist. Mammalia 48: 252-266.

Roberts, J.L., and P. Green. 1983. Breeding failure and decline of Merlins on a North Wales moor. Bird Study 30: 183-200.

Roff, D.A., and T.A. Mousseau. 1987. Quantitative genetics and fitness: Lessons from *Drosophila.* Heredity 58: 103-118.

Roskaft, E. 1985. The effect of enlarged brood size on the future reproductive potential of the Rook. J. Anim. Ecol. 54: 255-260.

Rubio Garcia, J.C., Rodriguez de los Santos, M., and R. Santa Rosa. 1983. Reproduction de la cigogne blanche (*Ciconia ciconia*) dans les marismas du Guadalquivir (Espagne). Alauda 51: 251-258.

Salisbury, E.J. 1942. The Reproductive Capacity of Plants. Bell, London.

Schaal, E.J. 1980. Reproductive capacity and seed size in *Lupinus texensis*. Amer. J. Bot. 67: 703-709.

Schemske, D.W. 1978. Evolution of reproductive characteristics of *Impatiens* (Balsaminaceae); The significance of cleistogamy and chasmogamy. J. Ecol. 59: 596-613.

Schluter, D., and J.N.M. Smith. 1986. Natural selection on beak and body size in the Song Sparrow. Evolution 40: 221-231.

Schmidt, K.P., and L.R. Lawlor. 1983. Growth rate projection and life history sensitivity for annual plants with a seed bank. Amer. Nat. 121: 525-539.

Shine, R. 1980. Ecology of Eastern Australian Whipsnakes of the genus *Demansia* . J. Herpet. 14: 381-389.

Simbotwe, M.P. 1980. Reproductive biology of the Skinks *Mabuya striata* and *Mabuya quinquetaeniata* in Zambia. Herpet. 36: 99-104.

Snedecor, G.W., and W.G. Cochran. 1967. Statistical methods. Iowa State University Press, Iowa.

Sokal, R.R., and F.J. Rohlf. 1981. Bionetry. 2nd. ed. Freeman, San Fransisco.

Stewart, J.R. 1979. The balance between number and size of young in the live bearing lizard *Gerrhonotus coeruleus*. Herpet. 35: 342-350.

Stiehl, R.B. 1985. Brood chronology of the Common Raven. Will. Bull. 97:

TABLE 1

PHENOTYPIC VARIABILITY OF FECUNDITY

Plants

Genus	Species	Mean	SD	CV	n	ref.
Anagallis	foemina	33.0	68.6	207.9	86	1
Arenaria	serpyllifolia	208.0	229.0	110.1	31	1
Arenaria	tenuifolia	69.4	49.9	71.9	48	1
Arum	maculatum	24.3	9.3	38.3	328	1
Bartsia	alpina	5.9	3.3	56.4	35	1
Bartsia	odontites	112.0	79.9	71.3	124	1
Bartsia	viscosa	21.3	13.9	65.3	172	1
Bellis	perennis	10.3	5.7	55.3	250	1
Campanula	glomerata	30.0	46.3	154.3	40	1
Capsella	simplex	158.3	145.0	91.6	100	1
Carduus	natans	19.5	8.3	42.6	43	1
Carlina	vulgaris	4.4	3.7	84.1	205	1
Centunculus	minimus	14.2	16.9	119.0	229	1
Cerastium	glomeratum	91.0	109.1	119.9	41	1
Cerastium	triviale	168.1	123.8	73.6	26	1
Chlora	perfoliata	13.4	25.8	192.5	180	1
Chrysanthemum	leucanthemum	14.1	12.5	88.6	100	1
Cicendia	filiformis	2.0	1.4	69.2	110	1
Coeloglossum	viride	9.0	3.8	42.2	44	1
Dianthus	armeria	22.8	26.0	114.0	131	1
Digitalis	purpurea	83.0	62.3	75.1	102	1

Genus	Species	Mean	SD	CV	n	ref.
Drosera	anglica	6.6	4.2	63.3	89	1
Drosera	intermedia	6.3	3.9	61.4	201	1
Drosera	rotundifolia	6.3	3.8	60.6	310	1
Epilobium	montanum	21.0	23.8	113.3	178	1
Epilobium	tetragonum	47.3	44.7	94.5	164	1
Erigeron	acre	16.4	30.2	184.1	161	1
Erophila	boerhaavii	17.4	9.5	54.6	25	1
Erophila	praecox	6.2	5.4	87.1	94	1
Erythraea	centaurium	43.4	55.5	127.9	173	1
Fragaria	vesca	1.6	1.1	68.8	20	4
Fragaria	virginiana	3.4	2.7	79.4	14	4
Gentiana	anglica	7.0	7.4	105.7	162	1
Gentiana	axillaris	17.2	10.8	62.6	214	1
Gentiana	baltica	5.5	3.9	70.9	54	1
Gentiana	germanica	8.0	7.0	87.5	141	1
Gentiana	pneumonanthe	2.7	1.1	41.0	181	1
Gymnadenia	conposea	15.4	8.2	53.2	159	1
Hutchinsea	petraea	99.0	93.4	94.3	36	1
Hyoscyamus	niger	18.2	20.5	112.4	136	1
Hypericum	acutum	160.0	198.3	123.9	33	1
Hypericum	androsaeum	117.0	80.1	68.5	29	1
Hypericum	dubium	180.0	219.3	121.8	43	1
Hypericum	hemifusum	68.8	61.2	89.0	65	1
Hypericum	hirsutum	355.9	253.5	71.2	51	1
Hypericum	perforatum	395.0	319.8	89.0	44	1
Hypericum	pulchrum	70.7	82.8	117.1	84	1
Hypericum	undulatum	149.0	175.0	117.4	11	1
Lapsana	communis	64.0	82.5	128.9	122	1
Linaria	minor	31.5	65.0	206.3	149	1
Linaria	elatine	102.0	170.0	166.7	83	1
Linaria	spuria	91.5	227.0	248.1	82	1
Linum	alpinum	26.1	23.2	88.9	40	1

Genus	Species	Mean	SD	CV	n	ref.
Linum	catharticum	27.3	65.9	241.4	252	1
Listera	ovata	38.7	13.8	35.7	29	1
Lobelia	urens	65.0	39.5	60.8	23	1
Ludwigia	leptocarpa	8.4	15.7	179.5	63	3
Lupinus	texensis	9.4	8.0	85.3	58	2
Luzula	pilosa	73.4	63.8	86.9	50	1
Lychnis	githago	12.7	8.8	69.3	141	1
Matricaria	suaveolens	43.0	64.0	148.8	164	1
Meconopsis	cambrica	14.7	13.6	92.5	102	1
Moenchia	erecta	2.8	2.2	78.6	217	1
Orchis	maculata	17.0	8.5	50.0	33	1
Papaver	argemone	6.8	7.4	108.7	227	1
Papaver	dubium	6.8	11.8	172.8	529	1
Papaver	hybridum	7.3	10.6	144.9	277	1
Papaver	rhoas	12.5	18.4	147.2	401	1
Parnassia	palustris	2.4	1.5	62.8	100	1
Primula	elatior	17.1	27.9	163.3	28	1
Rhinanthes	minor	17.3	18.8	108.7	171	1
Samolus	valerandi	44.3	50.0	112.9	55	1
Saxifraga	tridactylites	7.7	7.7	100.0	160	1
Senecio	vulgaris	24.7	33.0	133.6	448	1
Silene	anglica	16.9	20.2	119.5	48	1
Silene	dubia	122.4	107.4	87.7	10	1
Silene	conica	11.5	17.1	148.7	613	1
Silene	nodosa	235.0	187.0	79.6	61	1
Silene	otites	94.0	68.4	72.8	17	1
Silene	quinquevulnera	18.4	44.4	241.3	289	1
Solanum	nigrum	238.0	454.0	190.8	60	1
Sonchus	asper	105.0	75.5	71.9	25	1
Specularia	hybrida	13.3	27.1	203.8	169	1
Sysimbrium	thalianum	50.0	56.1	112.2	144	1
Taraxacum	officinale	13.3	9.4	70.4	400	1
Thlaspi	arvense	176.7	145.8	82.5	58	1
Tofieldia	palustris	8.7	2.3	26.4	56	1

Genus	Species	Mean	SD	CV	n	ref.
Verbascum	lychnitis	960.0	728.0	75.8	25	1
Verbascum	nigrum	1108.0	928.0	83.8	22	1
Verbascum	thapsus	226.0	380.0	168.1	37	1
Veronica	hybrida	16.1	11.5	71.7	121	1

Sources: 1-Salisbury (1942); 2-Schaal (1980); 3- Christy and Sharitz (1982); Jurik (1985)

Crustacea

Genus	Species	Mean	SD	CV	n	ref.
Anchialina	agilis	17.4	4.5	25.9	41	2
Cumopsis	goodsiri	32.2	11.0	34.2	110	1
Disatyloides	biplicata	26.3	6.4	24.3	32	1
Diastylis	goodsiri	159.9	17.1	10.7	39	1
Diastylis	polita	162.1	43.8	27.0	14	1
Diastylis	quadrispinosa	67.2	32.8	48.8	39	1
Diastylis	sclupta	65.4	14.7	22.4	101	1
Erythrops	elegans	5.6	3.4	60.7	11	2
Erythrops	serrata	12.4	6.1	49.2	42	2
Eudorella	pusilla	18.1	4.3	23.7	49	1
Gastrosaccus	lobatus	29.2	5.5	18.8	20	2
Hemilamprops	rosea	24.6	5.3	21.5	10	1
Hemimysis	lamornae	20.6	8.4	40.8	14	2
Iphinoe	serrata	44.7	14.9	33.3	20	1
Iphinoe	trispinosa	77.1	22.6	29.3	56	1
Lamprops	fasciata	23.5	6.1	26.0	44	1
Lamprops	fuscata	15.1	5.9	39.1	16	1
Lamprops	quadriplicata	168.5	20.1	11.9	10	1

Genus	Species	Mean	SD	CV	n	ref.
Leptomysis	gracilis	27.9	15.1	54.1	595	2
Leptomysis	lingvura	20.4	12.1	59.3	28	2
Leptostylis	longimana	20.9	5.6	26.8	102	1
Leucon	nasica	19.3	9.9	51.3	93	1
Mesodopsis	slabberi	8.8	3.2	36.4	30	2
Mysidopsis	didelphis	35.0	12.6	36.0	31	2
Mysidopsis	gibbosa	14.8	7.0	47.3	370	2
Mysis	mixta	30.3	16.7	55.1	46	2
Neomysis	integer	29.3	13.7	46.8	750	2
Pacifastacus	fortis	39.2	12.7	19.0	19	3
Paramysis	arenosa	12.5	5.8	46.4	484	2
Paramysis	flexuosus	26.8	9.5	35.4	565	2
Paramysis	inermis	22.5	11.8	52.4	853	2
Paramysis	neglectus	46.7	20.2	43.3	21	2
Schistomysis	kervillei	12.7	6.7	52.8	6762	2
Schistomysis	ornata	9.1	5.1	56.0	24	2

Sources: 1- Corey (1981); 2- Mauchline (1973); 3- Eng and Daniels (1982).

Amphibians

Genus	Species	Mean	SD	CV	n	ref.
Ambystoma	opacum	107.3	43.0	40.1	38	4
Ambystoma	texanum	262.0	61.0	23.3	14	5
Arthroleptis	poecilonotus	21.0	8.0	38.1	83	1
Bufo	maculatus	4809.0	1892.0	39.3	10	1
Bufo	regularis	10055.0	2885.0	28.7	11	1
Cynops	pyrrhogaster	11.3	1.9	16.8	23	8
Grymophelus	porphyritus	38.9	11.3	29.2	44	2
Hyla	japonica	717.9	278.3	38.8	32	8

Genus	Species	Mean	SD	CV	n	ref.
Hynobius	tsuensis	513.6	154.3	30.0	10	8
Hyperolius	nitidilus	303.0	96.0	31.7	14	1
Leptopelis	viridis	145.0	25.0	17.2	16	1
Onychodactylus	japonicus	11.3	1.9	16.8	23	8
Phrynobatrachus	accraensis	267.0	130.0	48.7	83	1
Phrynobatrachus	calcaratus	290.0	144.0	49.7	69	1
Phrynobatrachus	plicatus	1900.0	830.0	43.7	78	1
Ptychadena	oxyrhynchus	3476.0	1542.0	44.4	29	1
Rana	brevipoda	1695.6	702.7	41.4	38	8
Rana	japonica	1390.8	307.3	22.1	31	8
Rana	lemnocharis	2113.6	754.4	35.7	31	8
Rana	nigromaculata	2113.6	754.4	35.7	31	8
Rana	pipiens	443.9	117.4	26.4	45	3
Rana	tagoi	104.7	29.3	28.0	21	8
Rana	temporaria	1008.0	331.0	32.8	274	6
Rana	tsuschinensis	472.1	139.9	29.6	28	8
Rhacophorus	schlegelli	357.4	93.1	26.1	11	7

Sources: 1- Barbault (1984); 2- Bruce (1972); 3- Pettus and Angleton (1967); 4-Walls and Altig (1986); 5- Petranka (1984); 6- Gibbons and McCarthy (1986); 7- Okada (1966); 8- Kuramoto (1978).

Reptiles

Genus	Species	Mean	SD	CV	n	ref.
Agkistrodon	halys	8.1	2.70	33.3	19	1
Alligator	mississipiensis	30.3	9.70	32.0	14	20
Arizona	elegans	8.5	4.99	58.7	12	1
Calotes	versicolor	16.6	4.64	28.0	13	1
Caretta	caretta	117.2	19.50	16.6	235	18
Carphoris	vernis	3.3	0.98	29.7	43	7

Genus	Species	Mean	SD	CV	n	ref.
Carphoris	anoerius	2.9	0.86	29.7	14	7
Carphoris	helenae	3.7	1.12	30.3	14	7
Chelydra	asceola	5.0	4.13	82.6	115	9
Chrysemis	picta	7.6	3.52	46.3	128	17
Clonophis	kirtlandi	9.6	5.64	58.8	20	1
Cnemidophorus	tigris	2.1	2.01	95.7	45	11
Crotalus	horridus	12.6	2.00	15.9	16	3
Crotalus	viridis viridis	10.6	6.86	64.7	49	1
Crotalus	viridis heleri	7.9	3.98	50.4	12	1
Crotalus	viridis lutosus	7.9	2.96	37.5	38	1
Crotalus	viridis nuntius	7.0	2.46	35.1	10	1
Crotaphytus	collaris	7.6	4.37	57.5	39	1
Ctenotus	taeniolatus	3.7	1.17	31.6	42	14
Demansia	atra	7.5	2.42	32.3	12	19
Demansia	psamnophis	5.8	1.73	29.8	12	19
Diadophis	punctatus	3.9	1.44	36.9	300	24
Elaphe	obsoleta	15.2	9.12	60.0	16	1
Elaphe	vulpina	15.1	6.38	42.3	11	1
Eumeces	okadae	7.6	2.00	13.2	94	15
Eumeces	fasciatus	8.8	1.85	21.0	34	8
Farancia	abacura	32.2	20.80	64.6	23	1
Gerrhonotus	coeruleus	5.2	1.45	27.9	53	23
Goniocephelus	liogaster	3.2	0.85	26.6	22	1
Gopherus	polyphemus	7.0	1.70	24.3	47	6
Holbrookia	texana	5.0	0.87	17.4	208	1
Kinosternon	subrubrum	3.2	1.34	41.9	11	9
Lampropeltis	getulus	10.1	3.57	35.3	21	1
Lampropeltis	triangulum	10.3	3.45	33.5	20	1
Lycodon	aulicus	5.8	2.36	40.7	14	1
Mabuya	striata	4.2	1.34	31.9	20	5
Lycophidon	capense	4.4	1.67	38.0	19	1
Natrix	erythrogaster	15.5	6.45	41.6	20	1
Natrix	sipedon	25.7	11.92	46.4	27	1

Genus	Species	Mean	SD	CV	n	ref.
Opheodrys	aestivus	6.8	2.70	39.7	17	1
Opheodrys	vernalis	6.7	1.74	26.0	53	1
Philothamnus	hoplogaster	5.5	1.46	26.5	16	1
Phrynosoma	cornutum	29.0	5.33	18.4	56	11
Podocnemis	unifilis	27.3	5.70	20.9	12	22
Ptyas	mucosus	11.8	1.75	14.8	12	1
Regina	alleni	10.1	8.68	85.9	10	1
Regina	grahami	15.7	8.76	55.8	10	1
Regina	septemvittata	11.2	4.42	39.5	20	1
Rhinocheilus	lecontei	6.4	1.43	22.3	11	1
Sceloporus	clarki	19.6	4.81	24.5	32	13
Sceloporus	chrysostictus	2.5	0.79	31.6	14	1
Sceloporus	graciocus	3.6	0.98	27.2	57	1
Sceloporus	jarrovi	6.8	2.31	34.0	52	2
Sceloporus	malachiticus	4.6	1.83	39.8	19	1
Sceloporus	occidentalis	7.7	1.64	21.3	51	1
Sceloporus	undulatus	5.6	1.67	29.8	63	12
Sceloporus	variabilis	3.0	1.15	38.3	18	1
Sisteirus	catenatus	8.2	3.23	39.4	54	1
Sisteirus	miliarus	7.3	4.07	55.8	15	1
Sternotherus	odoratus	4.7	1.37	29.1	24	9
Sternotherus	minor	2.6	0.94	36.2	31	21
Tamnophis	radix	29.5	21.20	71.9	16	1
Tamnophis	sauritus	9.1	4.16	45.7	36	1
Tropidoclonion	lineatum	7.2	2.88	40.0	13	1
Urosaurus	ornatus	4.7	2.75	58.5	189	4
Uta	stansburiana	3.4	1.11	32.6	73	1
Virginiana	striatula	5.2	1.71	32.9	17	1
Virginiana	valeriae	6.6	2.70	40.9	20	1
Xenochrophis	piscator	40.1	17.70	44.1	19	1

Sources: 1-Fitch (1970); 2- Tinkle and Hadley (1973); 3- Gibbons (1972); 4- Dunham (1982); 5- Simbotwe (1980); 6- Landers et al (1980); 7- Clark

(1970); 8-Fitch (1954); 9-Iverson (1977); 10- Ballinger (1974); 11- Parker (1973); 12- Ballinger et al (1981); 13- Tinkle and Dunham (1986); 14- Taylor (1985); 15- Hasegawa (1984); 16- Pianka (1971); 17- Congdon and Tinkle (1982); 18- Frazer and Richardsson (1985); 19- Shine (1980); 20- Goodwin and Tinkle (1982); 21- Iverson (1978); 22- Foote (1978); Stewart (1979); 24- Fitch (1975).

Birds

Genus	Species	Mean	SD	CV	n	ref.
Arenaria	interpres	4.8	0.55	11.4	484	1
Accipiter	gentilis	3.6	0.69	19.0	132	1
Accipiter	nisus	5.0	0.77	15.5	729	1
Anas	platyrhynchos	12.5	2.11	16.9	95	1
Anas	strepera	9.9	1.84	18.5	73	1
Anser	fabalis	4.4	1.32	30.0	31	1
Aquila	chrysaetos	3.6	0.57	15.9	301	1
Aquila	pomarina	1.9	0.40	21.3	178	1
Ardea	cinerea	3.9	0.67	17.0	222	1
Aythia	ferina	9.4	1.82	19.3	142	1
Aythia	fuligula	10.8	2.41	22.3	72	1
Bonasa	bonasia	9.4	1.15	12.3	40	1
Branta	canadensis	5.9	1.39	23.6	75	1
Burhinus	oedicnemus	1.9	0.28	14.4	94	1
Buteo	buteo	2.5	0.70	27.7	130	1
Buteo	lagopus	3.8	1.07	28.0	64	1
Calidris	alpina	3.8	0.59	15.7	295	1
Calidris	maritima	3.9	0.28	7.2	82	1
Calidris	temminnkii	3.8	0.46	12.0	56	1
Charadrius	hiaticula	3.6	0.57	15.9	301	1
Charadrius	leschenaultii	3.0	0.37	12.5	22	1
Charadrius	morinellus	2.6	0.62	24.0	581	1
Charadrius	pecuarius	1.9	0.33	17.6	235	1

Genus	Species	Mean	SD	CV	n	ref.
Chetusa	gregaria	4.2	0.39	9.3	66	1
Ciconia	nigra	3.2	1.00	31.5	28	1
Circus	aeruginosus	4.6	1.11	24.1	200	1
Cygnus	colombianus	5.9	2.17	36.9	102	1
Egretta	egretta	4.8	0.69	14.3	199	1
Falco	columbarius	4.1	0.90	22.0	109	1
Falco	eleonorae	3.0	0.66	22.4	80	1
Falco	peregrinus	3.4	0.57	16.7	98	1
Falco	rusticolus	3.5	0.63	17.8	60	1
Falco	subbuteo	2.9	0.38	13.0	271	1
Falco	tinnunculus	4.7	1.00	21.3	523	1
Falco	vespertinus	3.5	0.70	20.1	65	1
Fulica	atra	7.1	1.83	25.7	1131	1
Gallinago	gallinago	3.9	0.49	12.5	284	1
Gallinula	chloropus	6.7	1.54	23.2	2278	1
Gavia	stellata	1.8	0.41	22.9	59	1
Gavia	arctica	1.9	0.37	19.8	78	1
Haematopus	ostralegus	2.8	0.65	23.5	636	1
Haliaeetus	albicella	2.1	0.54	25.5	57	1
Hieraeetus	fasciatus	2.0	0.33	16.8	53	1
Himanthopus	himanthopus	3.5	1.03	29.3	47	1
Histrionicus	histrionicus	5.7	1.33	23.3	77	1
Lagopus	lagopus	7.5	1.47	19.6	103	1
Lagopus	mutus	6.6	1.58	24.0	148	1
Larus	delavarensis	2.6	0.64	25.0	239	1
Larus	ichtyaetus	2.2	0.55	24.7	79	1
Larus	ridibundus	2.5	0.76	29.9	189	1
Limosa	limosa	3.9	0.35	9.1	145	1
Melanitia	nigra	6.8	1.18	17.3	50	1
Mergus	merganser	9.4	1.56	16.6	35	1
Mergus	serrator	9.2	1.75	19.1	149	1
Milvus	milvus	2.1	0.48	22.6	92	1
Numenius	arquata	3.8	0.50	13.2	127	1
Numenius	phaeopus	3.9	0.38	9.8	52	1

Genus	Species	Mean	SD	CV	n	ref.
Pandion	halieatus	2.6	0.68	25.9	172	1
Phalaropes	fulicarius	3.9	0.41	10.6	83	1
Phalaropus	lobates	3.9	0.41	10.6	83	1
Phoenicopterus	ruber	1.1	0.24	22.6	2000	1
Platalea	leucorodia	3.0	0.68	22.7	415	1
Pluvialis	apricaria	3.9	0.46	11.9	231	1
Podiceps	nigricollis	3.5	0.75	21.6	293	1
Porzana	porzana	10.3	1.25	12.1	51	1
Rissa	tridactyla	2.0	0.51	25.8	149	1
Scopolax	rusticola	3.8	0.53	13.8	462	1
Somateria	mallisima	4.6	0.97	21.0	193	1
Stercorarius	pomainus	2.0	0.22	11.3	244	1
Skua	skua	1.9	0.26	14.5	781	1
Tadorna	tadorna	8.8	1.57	17.8	95	1
Tetrao	urogallus	8.4	1.40	16.6	37	1
Tringa	tortanus	3.9	0.24	6.1	370	1
Vanellus	vanellus	3.9	0.49	12.7	558	1

Source: 1-Cramp (1977).

Mammals

Genus	Species	Mean	SD	CV	n	ref.
Calomys	callosus	4.5	1.80	40.0	25	21
Clethrionomys	gapperi	5.6	1.22	21.9	41	11
Didelphis	albiventris	4.2	1.40	33.3	10	12
Didelphis	marsupialis	4.5	1.36	30.2	41	12
Erinaceus	europaeus	5.2	2.00	38.5	85	13
Felix	catus	3.6	1.55	43.1	237	6
Galea	spixii	3.0	1.00	33.3	24	21
Kerodon	rupestris	1.5	0.66	44.0	76	7

Genus	Species	Mean	SD	CV	n	ref.
Martes	pernnanti	2.7	0.72	26.7	21	20
Meles	meles	2.9	0.89	30.7	37	19
Micromys	minutus	5.4	1.26	23.3	62	15
Microtus	breweri	3.4	1.10	32.4	102	14
Microtus	pennsylvaticus	5.6	1.22	21.8	41	11
Neomys	fodiens	6.3	2.78	44.1	18	4
Neotema	stephensi	1.1	0.31	28.1	78	9
Oryzomys	capito	3.9	1.05	26.9	14	17
Oryzomys	eliurus	3.0	1.30	43.3	18	21
Pitmys	subterraneus	2.8	0.85	30.4	149	5
Peromyscus	leucopus	4.3	1.13	26.3	128	2
Peromyscus	maniculatus	4.9	0.72	14.7	53	10
Proechimys	semispinosus	2.5	0.71	28.4	51	17
Scotinomys	teguina	2.3	0.64	27.8	21	16
Spermophilus	elegans	5.2	1.83	35.3	21	18
Suncus	marinus	2.1	1.45	69.0	211	3
Tatera	indica	4.8	1.38	28.8	71	8
Trichomys	apercoides	3.1	1.20	38.7	21	21
Vulpes	vulpes	4.1	2.05	50.0	29	1

Sources: 1- Allen (1984); 2- Lackey (1978); 3- Hasler et al (1977); 4- Michalak (1983); 5- Jemiolo (1983); 6- Legay and Pointier (1985); 7- Roberts et al (1984); 8- Jain (1984); 9- Vaughan and Czaplewski (1985); 10- Glazier (1985); 11- Innes and Millar (1981); 12- Tyndale-Biscoe and Mackenzie (1976); 13-Kristiansson (1981); 14- Tamarin (1977); 15- Harris (1979); 16- Hooper and Carleton (1976); 17-Fleming (1971); 18-Pfeifer (1982); 19- Neal (1977); 20- Powell (1982); 21- Streilein (1982).

TABLE 2

REGRESSION STATISTICS

For each regression analysis, the number of species included, the slope, its standard error, the probability that the slope equaled 0 (p = 0) or 1 (p =1), the intercept, and the proportion of the total variance in log S.D. explained by log mean are given.

TAXONOMIC GROUP	SPECIES (n)	SLOPE (a)	S.E.	P=0	P=1	INT. (b)	R^2
1. Plants	94	1.06	0.035	***	>0.05	-0.13	0.91
2. Reptiles	70	0.97	0.059	***	>0.05	-0.42	0.75
3. Crustacea	36	0.66	0.068	***	***	0.01	0.71
4. Amphibians	25	1.05	0.038	***	.0.05	-0.61	0.97
5. Mammals	27	0.84	0.131	***	>0.05	-0.40	0.58
6. Birds	79	0.91	0.088	***	>0.05	-0.70	0.58

*** $p<0.001$.

TABLE 3

CVs OF FECUNDITY

The taxonomic groups with the same subscript were not significantly different ($p > 0.05$) in terms of CVs as shown by Duncan's Multiple-range test. CVs were log transformed.

TAXONOMIC GROUP	SPECIES (n)	MEAN CV (%)	MIN. CV (%)	MAX. CV (%)	S.E. (CV) (%)
1. Plants^{a}	94	102.9	26.4	248.1	5.09
2. Reptiles^{b}	70	42.5	19.4	106.5	4.85
3. Crustacea^{b}	36	36.4	10.7	98.1	1.68
4. Amphibians^{b}	25	34.9	14.7	69.1	1.85
5. Birds^{c}	79	18.9	3.0	36.9	0.73

TABLE 4

VARIABILITY IN SUCCESSIVE AVIAN REPRODUCTIVE CHARACTERS

A. ALL NESTS

SPECIES	CLUTCH SIZE				NUMBER FLEDGED					
	X	SD	N	CV_c	X	SD	N	CV_f	CV_f-CV_c	ref.
1. Accipiter nisus	4.6	0.9	164	19.6	3.2	1.2	128	37.4	17.8	1
2. Anser caerulescens	4.7	1.0	183	21.6	4.1	1.1	183	24.9	3.3	2
3. Bubo bubo	2.6	1.0	42	24.3	2.0	0.9	50	43.6	19.3	3
4. Corvus corax	6.1	0.8	144	13.1	2.5	2.0	28	80.0	66.9	4
5. Corvus frugileus	3.6	1.0	42	27.8	0.9	1.1	42	122.2	94.4	5
6. Cygnus olor	7.7	1.3	50	16.8	3.6	2.6	50	72.2	55.4	6
7. Delichon urbica	4.0	0.7	144	17.8	3.5	1.0	144	27.2	9.4	7
8. Dendroica discolor	3.9	0.5	188	12.9	3.1	0.9	94	28.0	15.1	8
9. Ficedula hypoleuca	6.4	1.0	86	15.0	4.4	2.5	85	57.1	42.1	9
10. Lagopus l.	7.1	1.6	26	22.2	5.3	2.0	44	37.5	15.3	10
11. Parus cinctus	8.0	1.9	23	23.8	4.8	3.4	23	70.8	47.0	11
12. Parus ater	8.4	0.8	38	9.5	5.9	3.4	39	57.6	48.1	12
13. Parus caeruleus	8.8	1.3	67	14.8	5.2	3.4	64	65.4	50.6	12
14. Passer domesticus	5.0	0.8	443	16.5	2.0	1.9	473	93.5	77.0	13
15. Pica pica	6.4	1.1	116	17.2	2.0	2.3	116	115.0	97.8	14
16. Turdus pilaris	5.4	0.6	10	10.5	3.9	0.8	10	21.1	10.6	15

SPECIES	CLUTCH SIZE				NUMBER FLEDGED					
	X	SD	N	CV_c	X	SD	N	CV_f	CV_f-CV_c	ref.
17.Zonotrichia leucophrys	2.7	1.2	144	46.2	0.8	1.2	144	80.0	33.8	16
Mean				19.4				60.8	41.4	
S.E.				2.07				7.49	7.22	

B. SUCCESSFULL NESTS

SPECIES	CLUTCH SIZE				NUMBER FLEDGED					
	X	SD	N	CV_c	X	SD	N	CV_f	CV_f-CV_c	ref.
1.Bubo bubo	2.6	0.6	42	24.7	1.8	0.7	35	38.8	14.1	3
2.Buteo jamaicensis	2.5	0.8	53	30.4	1.6	1..2	53	72.0	41.6	17
3.Buteo lineatus	2.7	0.5	29	20.1	1.3	1.1	29	85.1	65.0	17
4.Chionis alba	2.4	0.7	114	29.8	2.0	0.7	68	36.0	6.2	18
5.Chionis minor	2.5	0.6	38	24.0	1.7	0.9	32	52.4	28.4	18
6.Ciconia ciconia	3.2	0.8	41	26.2	3.0	0.9	38	30.6	4.4	19
7.Falco columbarius	4.3	0.8	48	17.8	2.9	1.7	33	58.4	40.6	20
8.Gerygone igata	3.9	1.3	60	32.6	1.7	1.8	44	104.0	71.4	21
9.Moticella cinerea	4.9	0.7	203	14.2	3.9	1.2	89	31.2	17.0	22
10.Parabuteo unicinctus	3.0	1.3	60	22.4	1.9	0.8	46	42.3	19.9	23
11.Sethophaga ruticella	3.7	0.5	20	12.7	3.4	0.9	20	25.9	13.2	24
12.Strix uralinensis	2.9	1.1	57	36.5	2.7	1.0	57	37.3	0.8	25
13.Tyto alba	4.7	1.4	178	28.9	3.1	1.3	84	41.2	12.3	26

SPECIES	CLUTCH SIZE				NUMBER FLEDGED				
	X	SD	N	CV_c	X	SD	N	CV_f	CV_f-CV_c
Mean				24.6				50.4	25.8
S.E.				1.98				6.52	9.62

Sources: 1- Newton and Marquiss (1984); 2- Finney and Cook (1978); 3- Bergier and Badau (1979); 4- Stiehl (1985); 5- Roskaft (1985); 6- Birkhead et al (1983); 7- Bryant (1979); 8- Nolan (1978); 9- Alatalo and Lundberg (1984); 10- Hannon and Smith (1984); 11- Jarvinen (1982); 12- Blondel (1985); 13- Murphy (1978); 14- Reese and Kadlec (1985); 15- Wiklund (1985); 16- Petrinovich and and Pattersson (1983); 17- Wiley (1975); 18- Burger (1979); 19- Rubio Garcia et al (1983); 20- Roberts and Green (1983); 21- Gill (1982); 22- Tyler (1972); 23- Berdnarz (1987); 24- Morris and Lemon (pers. comm.); 25- Lundberg (1981); 26- Bunn et al (1982).

TABLE 5

VARIABILITY IN SUCCESSIVE REPRODUCTIVE CHARACTERS IN PLANTS

SPECIES	TRAIT 1				TRAIT 2					
	X	SD	N	CV_1	X	SD	N	CV_2	CV_2 -CV_1	ref.
1.Lupies texensis	14.2	10.6	90	74.6	9.4	8.0	58	85.3	10.7	1
2.Lupinus texensis	47.1	43.9	58	93.4	30.8	32.2	58	104.6	11.2	2
3.Impatiens pallida	37.1	51.7	37	139.4	19.6	34.1	37	174.0	34.6	3
4.Impatiens pallida	89.8	136.9	37	152.5	42.5	76.6	37	180.2	27.7	4
5.Discaria tomatou	264.0	393.0	40	148.9	17.0	26.0	40	152.9	4.0	5
6.Leptospermum scoparium	610.0	807.0	40	132.3	20.0	31.0	40	155.0	22.7	5
7.Aralia nudicaulis	79.0	16.4	30	20.8	38.0	21.9	30	57.6	36.8	6
8.Yucca whipplei	1744.0	586.4	58	33.6	162.0	76.2	58	47.0	13.4	7
9.Ludwigia leptocarpa	10.1	18.3	63	181.2	8.4	15.1	63	179.5	-1.7	8
10.Fragaria virginiana	5.5	3.3	20	60.0	3.4	2.7	20	79.4	19.4	9
11.Fragaria vesca	3.2	1.8	14	56.3	1.6	1.1	14	68.8	12.5	9
Mean				99.4				116.8	17.8	
S.E.				16.3				15.7	3.67	

Traits identification (trait 1 : trait 2) and source:

1- Inflorescences/plant : legumes/plant, Schaal (1980).
2- Seeds/plant : viable seeds/plant, Schaal (1980).
3- Cleistogamous buds/plant : cleistogamous seeds/plant, Schemske (1978).
4- Chasmogamous buds/plant : chasmogamous seeds/plant, Schemske (1978).

5- Flowers/plant : fruits/plant, Primack (1980).
6- Incipient fruits/plant : ripe fruits/plants, Edwards (1985).
7- Open flowers/plant : mature fruits/plant, Aker (1982).
8- Flowers/plants : fruits/plant, Christy and Sharitz (1980).
9- Flower buds/plant : ripe fruits/plant, Jurik (1985).

Figure1. Bivariate relationships between log SD and log mean fecundity in various organisms.

(a) herbaceous plants (fruit number)

(b) crustaceans (brood size)

(c) amphibians (clutch size)

(d) reptiles (clutch size)

(e) birds (clutch size, solid circles) and mammals (open circles).

FIG. 1A

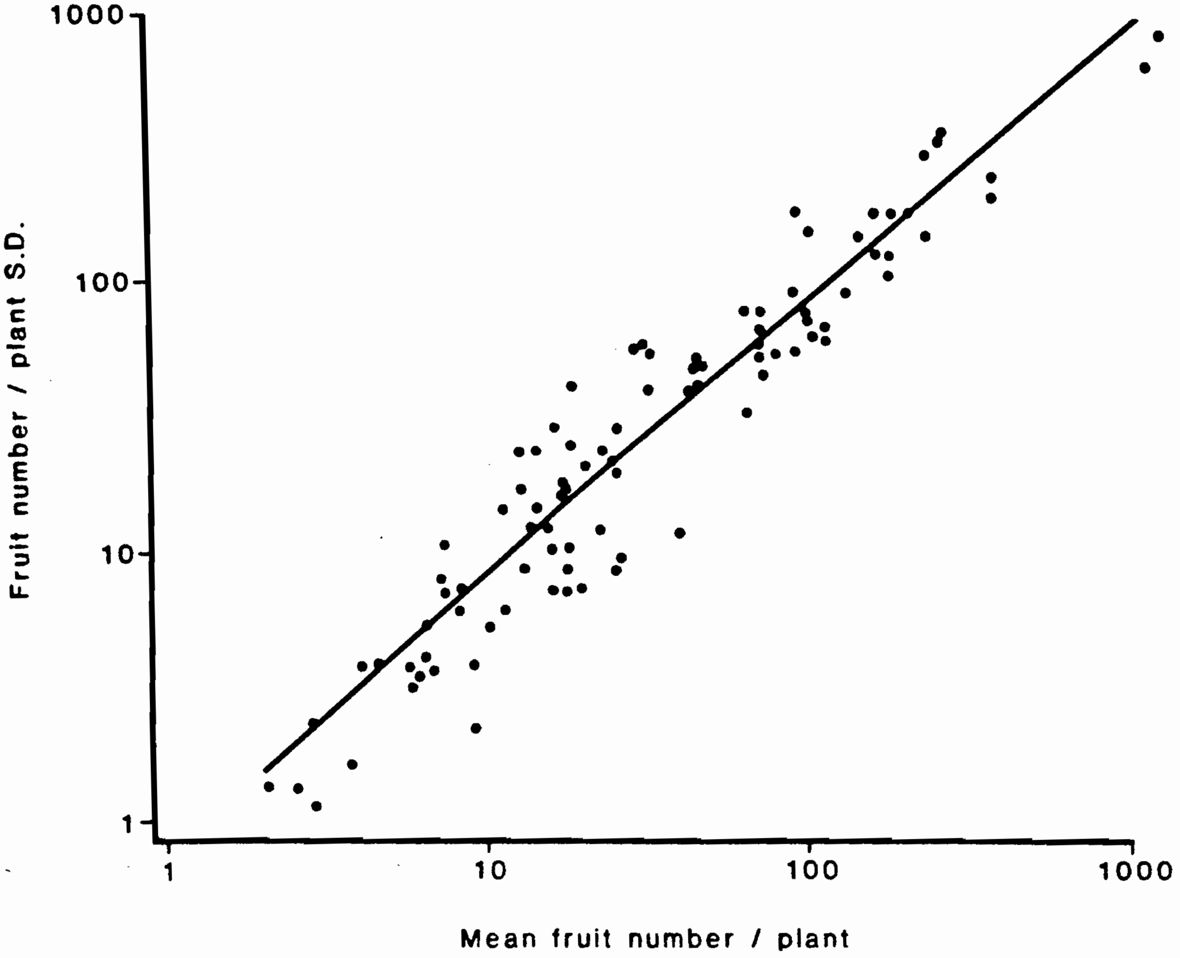

1000
100
10
1
Fruit number / plant S.D.
1
10
100
1000
Mean fruit number / plant

FIG. 1B

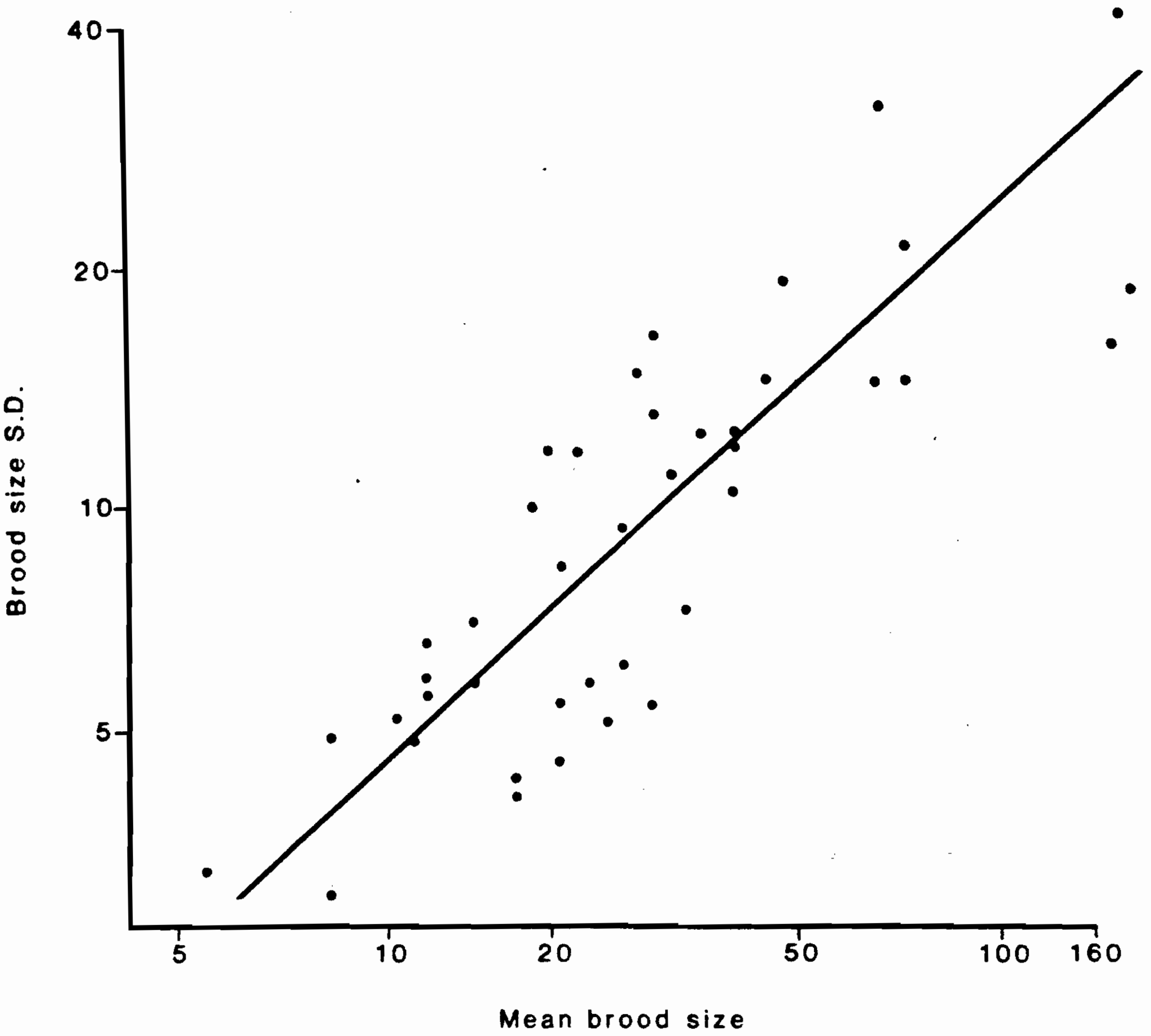


FIG. 1C

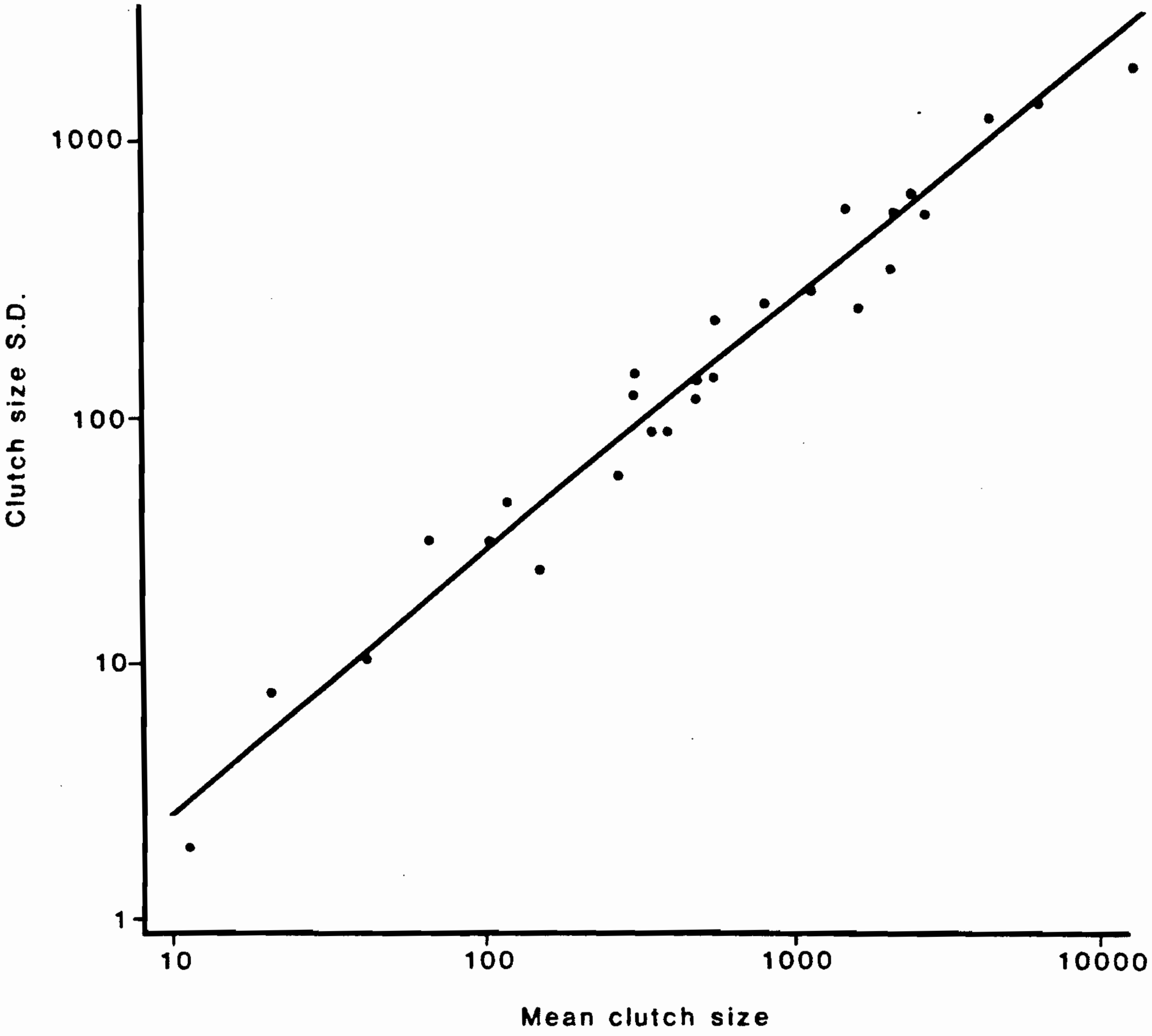

1000
100
10
1
Clutch size S.D.
10
100
1000
10000
Mean clutch size

FIG. 1D

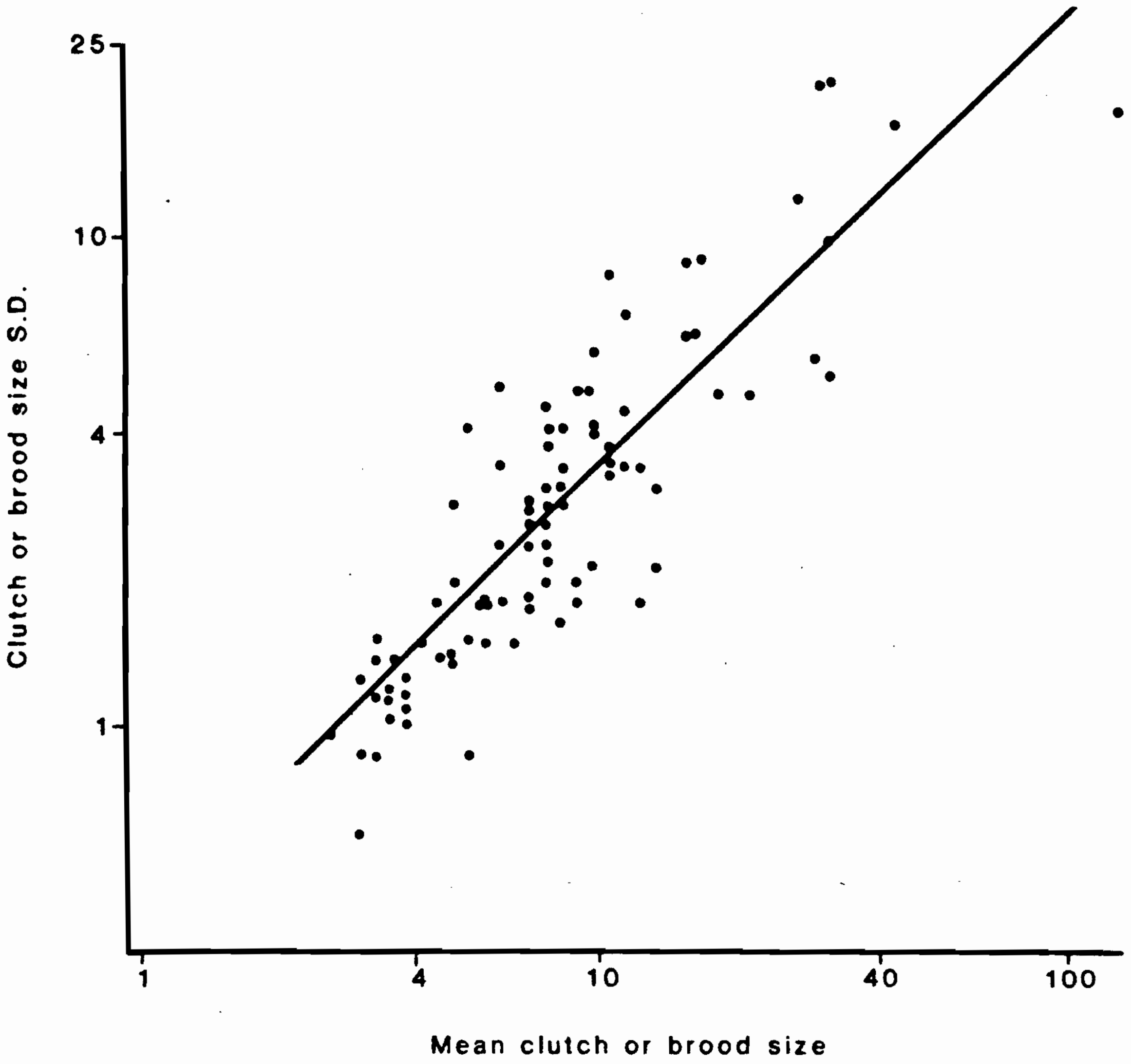

25
10
4
1
1
4
10
40
100
Clutch or brood size S.D.
Mean clutch or brood size

FIG. 1E

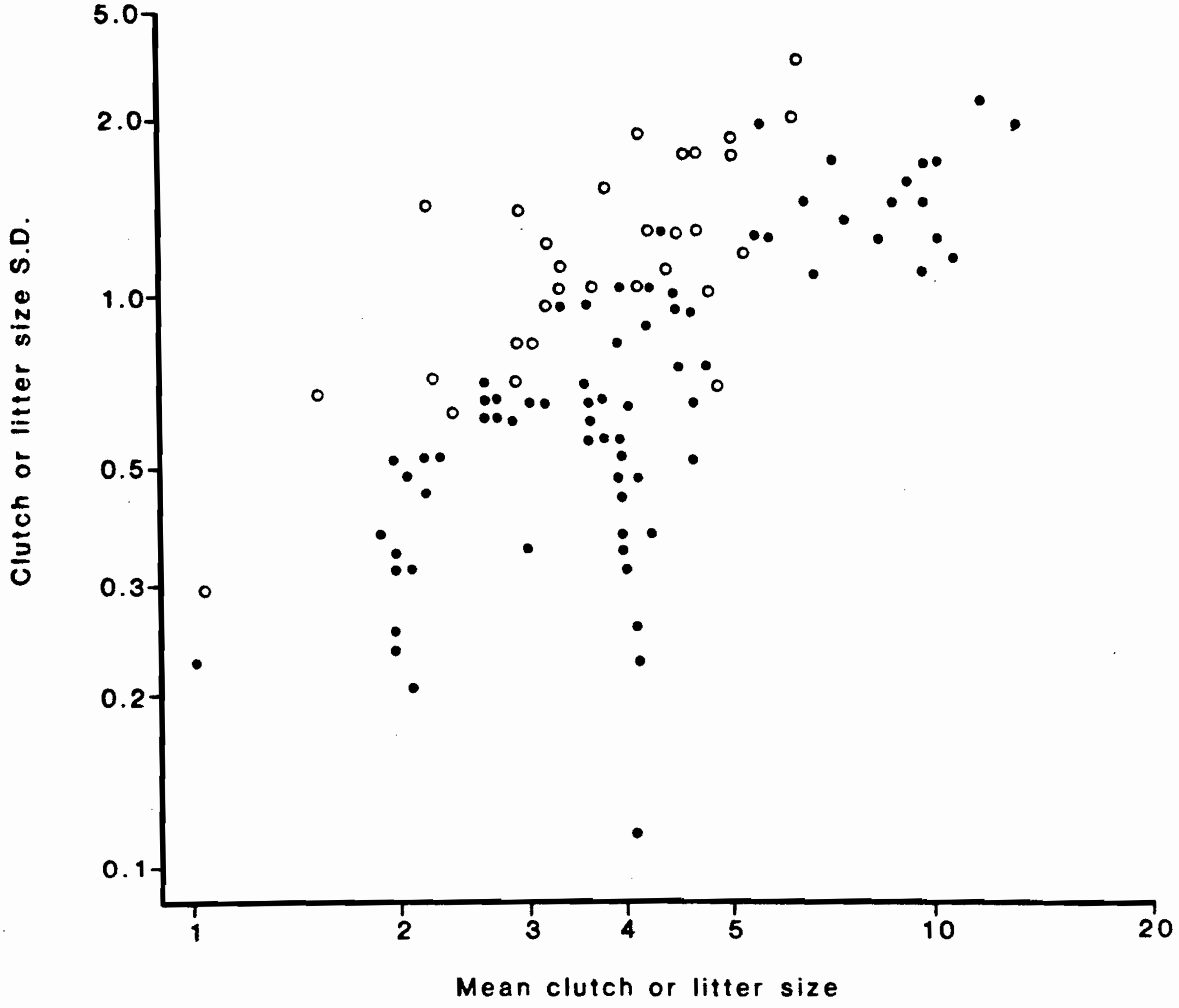

5.0
2.0
1.0
0.5
0.3
0.2
0.1
Clutch or litter size S.D.
1
2
3
4
5
10
20
Mean clutch or litter size

Figure 2. Predicted relationships between log S.D. and log mean for fecundity in plants, crustacea, amphibians, reptiles, birds, and mammals.

FIG.2

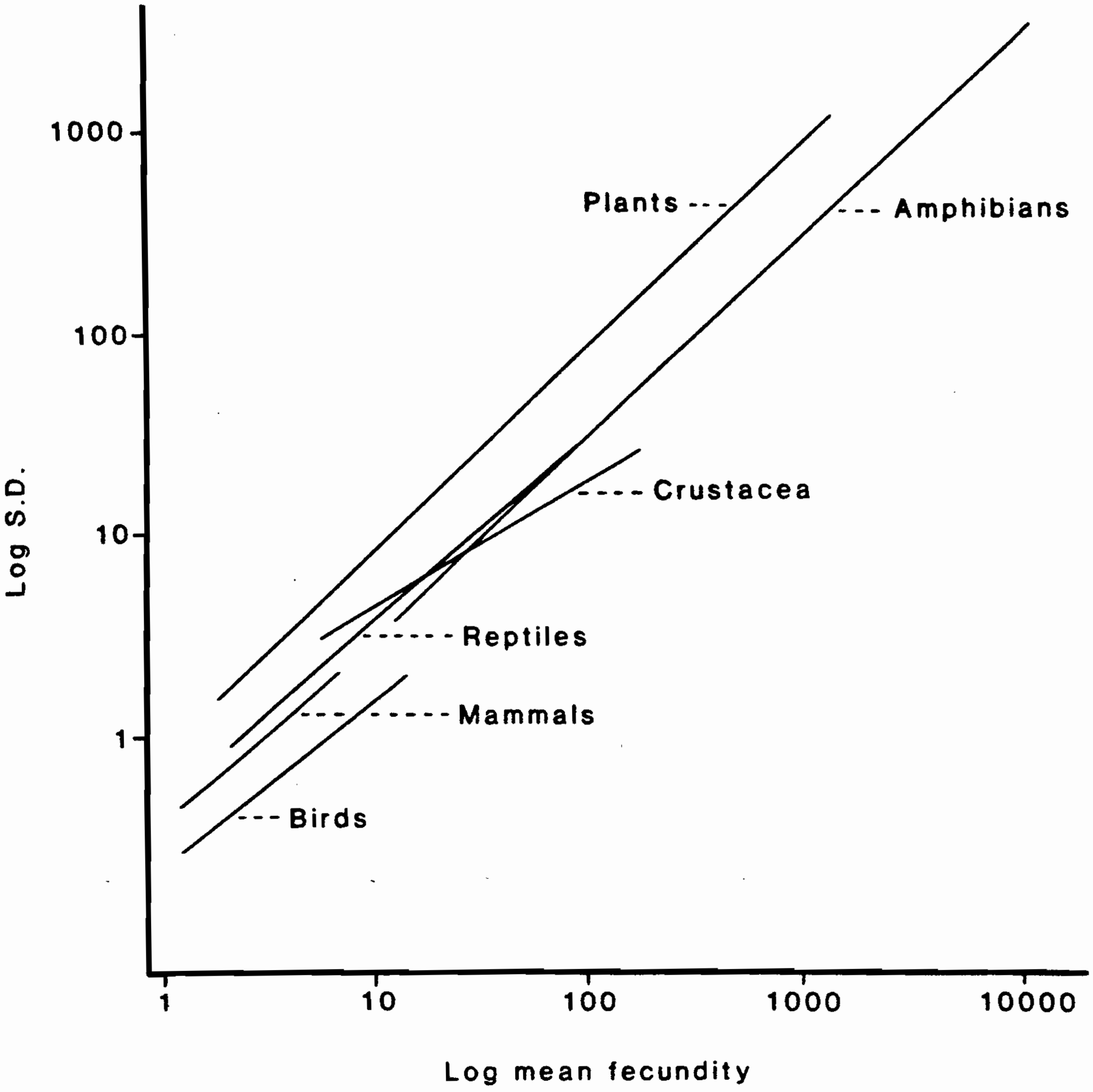

1000
100
10
1
Log S.D.
1
10
100
1000
10000
Log mean fecundity
Plants
Amphibians
Crustacea
Reptiles
Mammals
Birds

Figure 3. Frequency distribution of CVs of fecundity in (a) plants; (b) crustaceans; (c) reptiles; (d) amphibians; (e) mammals; (f) birds.

FIG.3

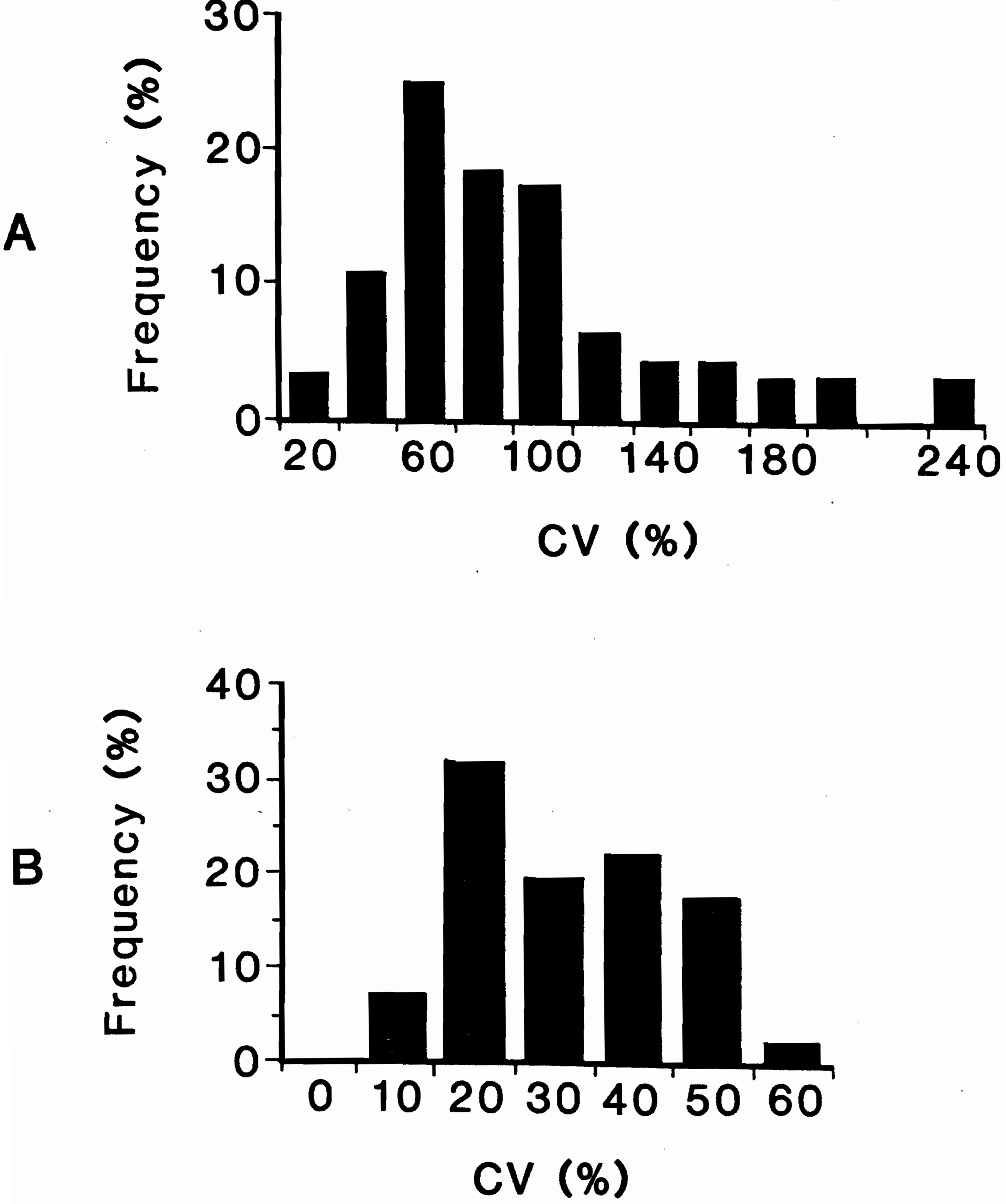

A
Frequency (%)
30
20
10
0
20
60
100
140
180
240
CV (%)
B
Frequency (%)
40
30
20
10
0
0
10
20
30
40
50
60
CV (%)

FIG.3

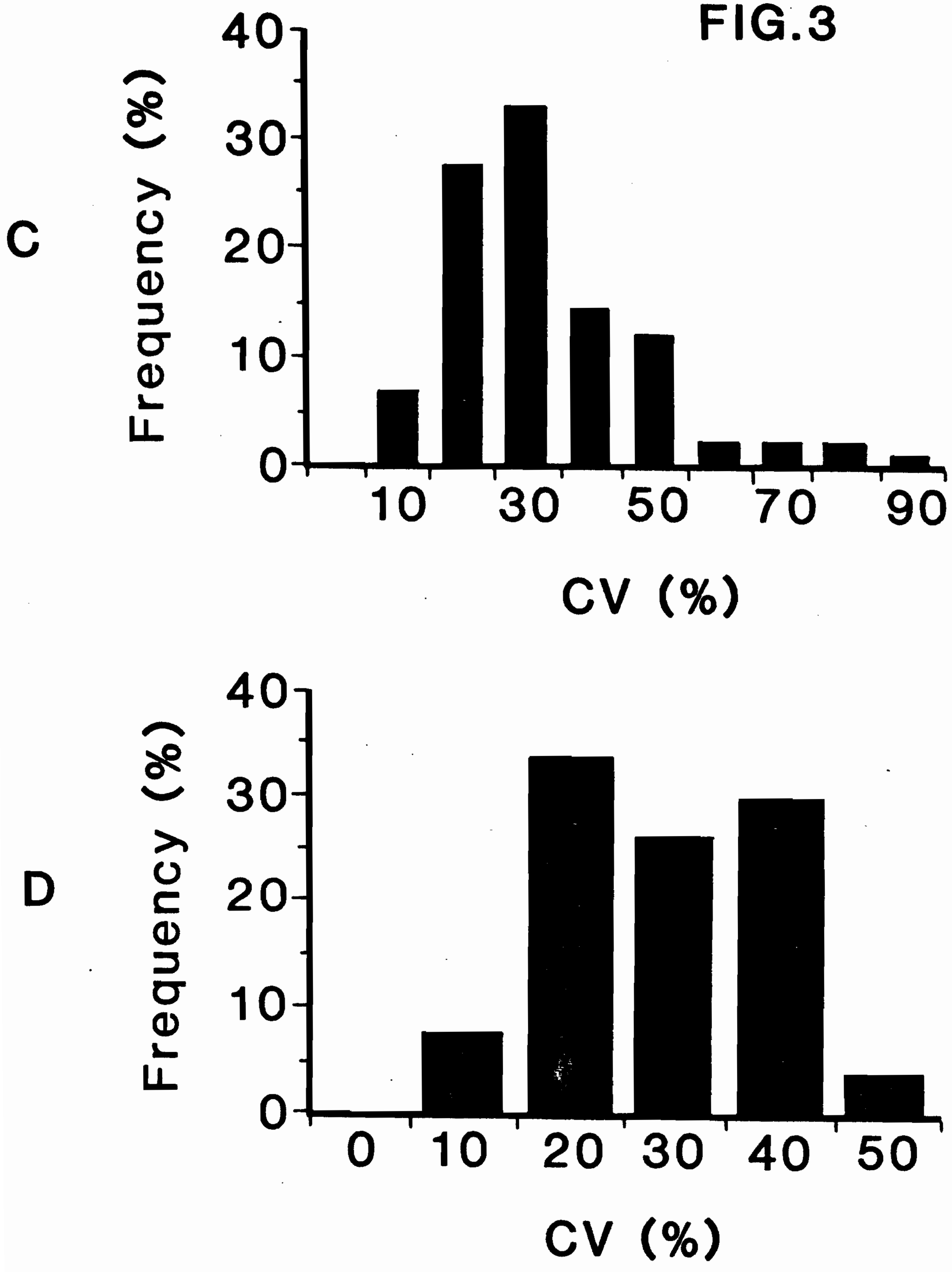
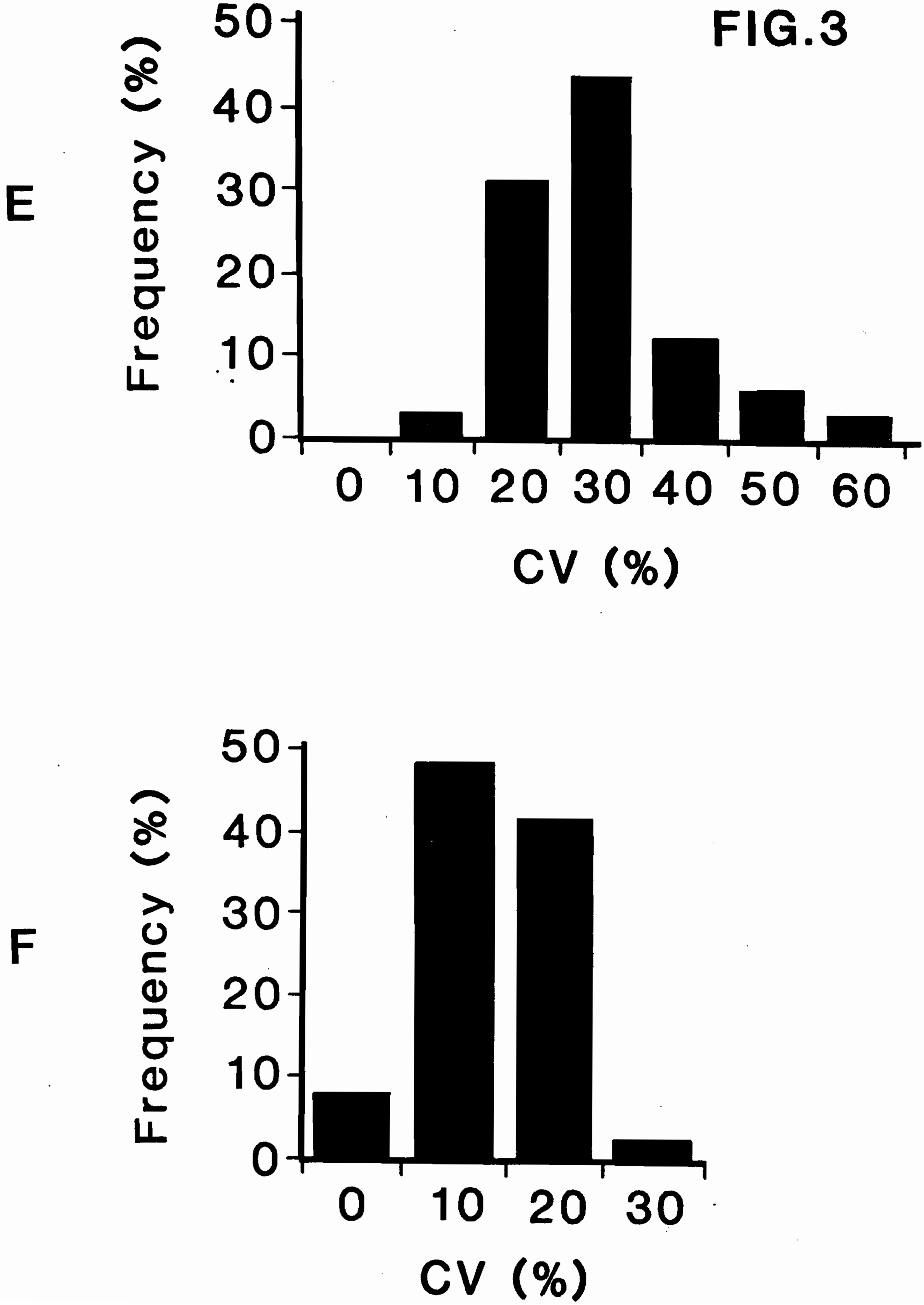

C
Frequency (%)
0
10
20
30
40
10
30
50
70
90
CV (%)
D
Frequency (%)
0
10
20
30
40
0
10
20
30
40
50
CV (%)

FIG.3


E
Frequency (%)
50
40
30
20
10
0
0
10
20
30
40
50
60
CV (%)
F
Frequency (%)
50
40
30
20
10
0
0
10
20
30
CV (%)

CHAPTER 5

PHENOTYPIC VARIABILITY OF FECUNDITY
IN
ANNUAL AND PERENNIAL PLANTS

ABSTRACT

In this paper, the relationship between the phenotypic variability of fecundity (fruit number per plant) and life history (annual or perennial) was investigated in 50 annuals and 40 herbaceous perennial species Phenotypic variability was measured with the Coefficient of Variation (CV = S.D./Mean). For a subset of the data, Skewness was also calculated. The results showed that both CV and Skewness were significantly greater in annuals than in perennials. The pattern of contribution to the population reproductive output by individuals of different fecundities was also investigated. In annuals, individuals in the lowest fecundity class (bearing the fewest fruits) contributed most to the total population output. In perennials, individuals from this same fecundity class contributed much less and the greatest contribution was that of individuals of intermediate fecundity. These results are discussed in the light of the theory of the cost of reproduction.

INTRODUCTION

An increasing amount of research has been devoted recently to the study of the variation of life history characters within populations. Some theories have sought to clarify the adaptive value of phenotypic variability in characters related to fitness (e.g. Gillespie 1970; Lacey et al 1983), while others have explored the demographic consequences of fitness variability itself (Arnold and Wade 1984; Heywood 1986). There are, however, very few comparative studies on the phenotypic variability of life history characters within populations [but see Kluge (1981) and Harfernick and Garrison (1986) for zoological examples]. In a literature review, Cabana and Bell (1987) have found that the variability of individual fecundity in natural populations of herbaceous annual and perennial plants was much higher than in other groups of organisms, including crustacea, amphibians, reptiles, birds, and mammals. Variability of plant fecundity, measured as the Coefficient of Variation (CV=100* S.D./mean) of the number of fruits per individual plant, also differed greatly among plant species, ranging from 36% to 251%. These large differences in phenotypic variability of plant fecundity beg for an explanation. In the present paper, we test two simple alternative hypotheses relating the variability of fecundity to differences in life history between annuals and perennials.

Iteroparous perennials differ from annuals in that their reproductive life can span several years instead of being limited to a single season . In plants, it is well known that fecundity (fruit or seed number) is generally well correlated with size (e.g. Gottlieb 1977; Leverich and Levin 1979; Kawano and Masuda 1980; Lovett Doust 1986). Given their potentially longer growing period, we can expect perennials to exhibit a larger size variability than annuals, especially if several cohorts are simultaneously present in the population. Our first hypothesis therefore simply states that CV of plant fecundity should be greater in perennials than in annuals because of this greater size variation.

Our second hypothesis involves a fundamental concept in the interpretations of life history strategies, the cost of reproduction (Bell and Koufopanou 1986). Semelparity and iteroparity have been suggested to be responses to different balances between the benefits and costs of repeated reproduction (Gadgil and Bossert 1970; Bell 1980). Among annual plants, all resources should eventually be allocated to reproduction, since lower levels of reproductive effort do not entail any potential benefits in the form of increased future reproduction or survival. In annuals, therefore, all individuals are expected to reproduce, irrespective of the cost incurred, and variability in reproductive potential between individual, due to size variation, for example, should be fully expressed. On the other hand, maximum reproductive effort may not be the best strategy for all indidividuals in a perennial species if delayed reproduction, or lower reproductive effort, can lead to an increase in future survival or reproduction. Thus, size thresholds, below which plants do not reproduce, have been reported in a number of perennial species (e.g. Tamn 1956; Kachi and Hirose 1983; Kingsolver 1986). Such size dependent determination of reproductive status suggests that in perennials the distribution of the size of reproducing individual should be truncated to the left, leading to a lower size variability of reproducing individuals compared to the that of the whole population. Thus, if fecundity is related to plant size, the temporal contraint hypothesis would predict that C.V. of fecundity should be higher in annuals than in perennials. In the present paper, I will test these two alternative hypotheses using literature and original data on the variability of fecundity in natural populations of herbaceous annuals and perennials.

METHODS

Data

The mean and standard deviation (S.D.) of the number of fruits per plant in 80 species of herbaceous annuals and perennials were obtained from Salisbury (1942). The term "fruit" is taken here in a broad sense, and structures like fruiting heads (e.g. in *Taraxacum officinale* , Salisbury 1942, p.161) were considered as fruits. The species for which data were obtained from Salisbury (1942) were: Annuals:*Anagallis foemina, Arenaria tenuifolia, Bartsia odontites, B. viscosa, Bidens tripartita, Capsella simplex, Cardamine hirsuta, Carduus natans, Centuculus minimus, Cerastium glomeratum, C. semidecandrum, Cicendia filiformis, Dianthus armeria, Erophila boerhaavii, E. praecox, Gentiana axillaris, Hypochoeris glabra, Lapsana communis, Linaria elatine, L. minor, L. spuria, Linum catharticum, Matricaria suaveolens, Moenchia erecta, Papaver argemone, P. dubium, P. hybridum, P. rhoas, Rhinans minor, Saxifraga tridactylites, Senecio vulgaris, Silene conica, S. quinquevulnera, Sonchus asper, S. oleraceus, Specularia hybrida, Sysimbirium thalianum, Solanum nigrum, Thlaspi arvense, Veronica hederaefolia.* ; Perennials: *Allium ursinum, Arum maculatum, Bellis perennis, Bartsia alpina, Cerastium triviale, Coeloglossum viride, Circaea lutetiana, Chrysanthemum leucanthemum, Drosera anglica, D. intermedia, D. rotundifolia, Epilobium montanum, E. tetragonum, Gentiana pneumonanthe, Gymnadenia conopsea, Habenaria chlorantha, Hypericum acutum, H. dubium, H. hirsutum, H. montanum, H. pulchrum, H. undulatum, Linum alpinum, Listera ovata, Lobelia urens, Luzula pilosa, Meconopsis cambrica, Melampyrum pratense, Orchis maculata, Parnassia palustris, Plantago media, Primula elatior, P. farinosa, Silene dubia, S. otites, Scrophularia nodosa, Taraxacum oficinale, Tofeldia palustris, Verbascum nigrum* . Additional data on 10 herbaceous annuals from disturbed habitats were collected in the field. Individual plants were harvested from September to October 1984 in downtown

Montreal. The harvesting procedure consisted of collecting all individuals contained in a 1 m^2 grid situated roughly at the center of the population until 200 plants were obtained. If that number was not attained with the first grid harvesting was continued in an adjacent grid, and so on until the quota was achieved. Plants were then brought to the lab where the number of fruits per plant was counted. The species investigated were *Brassica kaber*, *Capsella bursa-pastoris*, *Galinsoga ciliata*, *Lepidium denisiflorum*, *Matricaria matricarioides*, *Medicago lupulina*, *Senecio vulgaris*, *Sonchus asper*, *Thlaspi arvense*, *Trifolium arvense*.

Analysis

I calculated the CV (100 * S.D./Mean) of the number of fruits per plant for each species. Previous work (Cabana and Bell 1987) has shown this index of variability to be independent of mean plant fecundity. Thus, CV of species with different mean fecundity can be compared without incurring any systematic bias. Skewness (g_1, Sokal and Rohlf 1981) was calculated from the Montreal data and also in the cases where the frequency distributions of fruit number per plant were reported by Salisbury. Information on life history was obtained from Butcher (1961) and Marie-Victorin (1964). The effect of life history on mean, CV and Skewness of fecundity was investigated with t-tests (Sokal and Rohlf 1981). These variables were log-transformed, as this transformation was found to normalize the data and eliminate heteroscadisticity.

RESULTS

Mean fruit number per plant did not significantly differ between annuals and perennials (Table 1). However, herbaceous annuals had significantly higher CVs for fruit number than herbaceous perennials (Table 1 and Figure 1), thus confirming the temporal constraint hypothesis, but falsifying the age-classes hypothesis. No annual species showed CVs of fecundity smaller than 50% while 8 (20%) perennials had CVs between 11% and 50%. Annuals with CVs greater than 100% (31 species or 62%) were relatively more numerous than perennials with equivalent CV (8 species or 20%). Overall, CV averaged 122.8% in annuals, and 77.6% in perennials. All annual and perennial species were significantly (Snedecor and Cochrane 1967: Table X) positively skewed at the 0.05 level (Table 1 and Figure 2,). Thus, a distribution characterized by a large number of individuals with low fruit production and a small number of highly fecund individuals seem to be the rule in herbaceous plants. Differences between annuals and perennials in skewness were more dramatic than in the case of the CVs : no perennial species had Skewness greater than 2, while 70 % (26/37) of annuals exceeded that value; the overall difference in skewness was significant ($p<0.001$; Table 1). No significant relationship (Spearman Rank Correlation $r_S = 0.12$, $p>0.05$) between Skewness and mean fruit number was found. Skewness therefore needed not to be scaled for differences in mean when comparing species with different mean fecundities. This statistical finding contrasts with that of Turner and Rabinowitz (1983) who found Skewness to be positively related to mean plant size in monocultures of *Festuca paradoxa* . Thus, scaling rules for the moments of the distributions of fecundity or size at the intraspecific level therefore should not be extrapolated to other traits or taxonomic levels. Positive skewness is a characteristic of the log-normal distribution (Sokal and Rohlf 1981) which has been tentatively fitted to biological variables such as plant size (e.g. Turner and Rabinowitz 1983). I tested the adequacy of this distribution as a general model for fecundity distribution in natural plant population by testing the normality of the log-transformed fecundity data with a Kolmogorov D test (Sokal and Rohlf 1981) (Figure 3). Only 25% of the 52 annual and perennial species were found to be normally distributed on the logarithmic scale (at the 0.05 significance level). Thus the simple log-normal model for the distribution of plant fecundity did not apply to the majority of the herbaceous species included in the present study.

The skewed distribution of fecundity among herbs has led to the conclusion that "relatively few individuals contribute most of the offspring from which future generations will be drawn" (Dolan 1984). On the other hand, as was pointed out by Schaal (1980), highly skewed fecundity distributions can also have the consequence that, viewed at the whole population level rather than at the individual plant level, most of the fruit (or seed) production is due to the many individuals producing few fruits (or seeds). Whether a randomly selected zygote has a greater or smaller probability of originating from parents with high fecundity than from ones with low fecundity will depend on the relationship between plant fecundity and frequency. For example, highly fecund individuals may occur at such low frequency that their total contribution to the population reproductive output would be smaller than that of the much more numerous individuals bearing only a few fruits. Conversely, it is possible that the frequency of highly fecund individuals might not be so low as to offset their greater fecundity, so that their contribution to the population output would then be greater than that of the individuals bearing only a few fruits. Measures of CV and Skewness do not provide clear means of distinguishing between these two alternative patterns of contribution to the population output. To further explore this problem, I have calculated for each species the relative contribution of ten equally spaced fecundity classes by defining the range of each of 10 increasingly higher fecundity classes as the species' observed range in individual fecundity divided by 10. For each class, the relative contribution to the total population fecundity was then estimated as the sum of the number of fruits produced by all the individuals belonging to the class divided by the total number of fruits produced by the whole population.

The resulting relationship between relative contribution and the order of fecundity class (1 to 10) indicates whether an offspring randomly selected from the population is more likely to descend from a maternal parent with high fecundity than from one with low fecundity. Equal contribution of all fecundity classes would be indicated by a horizontal line at contribution of 10%. The relationships between mean relative contribution and the order of fecundity class differed strikingly between annuals and perennials (Chi-square = 31.2, d.f. = 9. $p < 0.001$, Figure 3). In annuals, relative contribution declined more or less monotonically with fecundity class, decreasing from an average value of 28% in class 1, to values between 4 and 8% in classes 8-10. Relative contribution to the population fruit pool therefore declined when individuals progressively more fecund are considered, reflecting the fact that that higher fecundity of some individuals did not compensate for their low frequency. In annuals, therefore, a randomly selected individual is more likely to have originated from one of the numerous plants with low fecundity than from a highly fecund individual. Perennials behave quite differently. The mean relative contribution was low (6%) amongst the least fecund individuals (class 1), sharply increased to a reach a maximum (18%) in class 3, and then declined in higher classes. Relative contribution in perennials was significantly smaller than in annuals in class 1 (t-test with arcsin transformation : $t = 5.46$, $p < 0.001$), and higher in classes 4 and 6 (respectively $t = 3.87$, $p < 0.001$ and $t = 2.44$, $p < 0.05$). Thus in contrast with annnuals, intermediate rather than low fecundity individuals make the greatest contribution to overall population reproduction in perennials.

DISCUSSION

I have shown that the distribution of individual fruit production in annuals differed from that of perennials in having greater CV and positive Skewness, with the consequence that the greater contribution to total population reproduction is made by the lowest fecundity class in annuals, but by the intermediate classes in perennials.

These results support the hypothesis of a relationship between phenotypic variability and the restriction of life span in annuals. Like obligate annuals, long-lived monocarpic species reproduce once and then die, but, unlike them, their age at reproduction can be highly variable (Schaffer 1974; Werner and Caswell 1977; Inouye and Taylor 1980). Werner and Caswell's (1977) observation than in Teasel (*Dipsacus sylvestris*), a long-lived monocarp, the switch to reproduction was better explained by plant size than age suggests that such species can "wait" until external or internal conditions are optimal for reproduction. We would therefore expect the phenotypic variability of fecundity in long-lived monocarp to be closer to that of perennials having also reproductive size thresholds and plastic age at maturity than to that of obligate annuals. I could obtain the relevant data to test this corollary hypothesis for only one species, *Yucca whipplei* , in Aker (1982), who presents means and standard deviations for the number of mature fruits per plant. In three populations, the CVs for this character were 47.0, 49.5, and 55.9%, and, while each of these values cannot be statistically considered as not belonging to the frequency distribution of CV in annuals (t-tests using S.D. of the distribution of CVs as denominator: all $p > 0.05$), only 3 annual species (6%) had CVs smaller than the most variable population of *Yucca*. On the other hand, these same three values fell well within the range of CVs in perennials (Table 1). Thus, high phenotypic variability of plant fecundity would seem to be related to the existence of constraints on life span rather than to semelparity *per se*.

The present results also suggest that in herbaceous perennials, age-related changes in fecundity were not large enough to lead by themselves to high variability at the whole population level. This, however, might may not apply to woody perennials. Primack (1980) noted that in three species of montane shrubs, reproductive individuals ranged in size from being as large as small trees to being as small as prostrate plants. In two of these species for which data on fruit production were available, *Discaria tomatou* , and

Leptospermum scoparium , CVs averaged respectively 126 and 173%, which represent high values for perennials (Figure 1), and, in the case of *Leptospermum* , constituted a significant departure from the distribution of CVs in herbaceous perennials (t = 2.85, p <0.01). Further data on the variability of fecundity in natural populations of woody perennials, if available, would certainly help in establishing the generality of this result.

To conclude, I have described statistical aspects of the frequency distribution of plant fecundity in relation to life history (annuals *vs* perennials). It is noteworthy that no significant difference in mean fruit number was found between annuals and perennials, while CV and Skewness clearly differed between them. This suggests that valuable information can be obtained not only from measures of central tendency, like the mean, but also from statistics of variation like the CV and Skewness. Empirical studies of phenotypic variability can also be used as "yardstick" in the evaluation of the degree of variability to expect *a priori* in a particular species. For example, a CV of 20% for fruit number would represent an exceptionally low level of variability in an annual, and such an observation would in turn warrant further investigation to explain the high degree of canalization in fecundity that would exhibited by this hypothetical species.

LITERATURE CITED

Aker, C.L. 1982. Regulation of flower, fruit and seed production by a monocarpic perennial,*Yucca whipplei*. J. Ecol. 70: 357-372.

Arnold, S.J., and Wade, M.J. 1984. On the measurement of natural and sexual selection: theory. Evolution 38: 709-719.

Bell, G. 1980. The costs of reproduction and their consequences. Amer. Nat. 116: 45-76.

Bell, G., and Koufopanou, V. 1987. The cost of reproduction. Oxford Surv. Evol. Biol. 3: 83-131.

Butcher, R.W. 1961. A New Illustrated British Flora. Vol. I-II. Leonard Hill ltd. London.

Cabana, G. and Bell, G.1987. The phenotypic variability of fecundity. MS.

Dolan, R.W. 1984. The effect of seed size and maternal source on individual size in a population of *Ludwigia leptocarpa* (Onagraceae). Amer. J. Bot. 71: 1302-1307.

Gadgil, M., and Bossert, W.H. 1970. Life historical consequences of natural selection. Amer. Nat. 104: 1-24.

Gillespie, J.H. 1977. Natural seletion for variance in offspring number: A new evolutionary principle. Amer. Nat. 111: 1010-1014.

Gottlieb, L.D. 1977. Genotypic similarity of large and small individuals in a natural population of the annual plant *Stephanomeria exigua* ssp. *coronaria* (Compositae). J. Ecol. 65: 127-134.

Hafernick, J.E. Jr., and Garrison, R.W. 1986. Mating success and survival rate in a population of damselflies: results at variance with theory? Amer. Nat. 128: 353-365.

Heywood, J.S. 1986. The effect of plant size variation on genetic drift in populations of annuals. Amer. Nat. 127: 851-861.

Inouye, P.W., and Taylor, O.R. 1980. Variation in generation time in *Frasera speciosa* (Gentianaceae), a long-lived perennial monocarp. Oecologia 47: 171-174.

Kachi, N., and Hirose, T. 1985. Population dynamics of *Oenethera glazioviana* in a sand-dune system with special reference to the adaptive significance of size-dependent reproduction. J. Ecol. 73: 887-901.

Kawano, S., and Masuda, J. 1980. The productive and reproductive biology of flowering plants. VII. Resource allocation and reproductive capacity in wild populations of *Helionopsis orientalis* (Thumb.) C. Tanaka (Liliaceae). Oecologia 45: 307-317.

Kingsolver, R.W. 1986. Vegetative reproduction as a stabilizing feature of the population dynamics of *Yucca glauca* . Oecologia 69: 380-386.

Lacey, E.P., Real, L., Antonovics, J., and Heckel, D.G. 1983. Variance models in the study of life histories. Amer. Nat. 122: 114-131.

Leverich, W.J., and Levin, D.A. 1979. Age-specific survivorship in *Phlox drummondi*. Amer. Nat. 113: 881-903.

Lovett Doust, L., Lovett Doust, J., and Turi, K. 1986. Fecundity and size relationships in Jack-in-the-pulpit, *Arisaema triphyllum* (Araceae). Amer. J. Bot. 73: 489-494.

Marie-Victorin, Fr. 1964. Flore laurentienne. 2ème ed. Les Presses de l'Université de Montréal, Montréal.

Primack, R.B. 1980. Variation in the phenology of natural populations of montane shrubs in New Zealand. J. Ecol. 68: 849-862.

Salisbury, E.J. 1942. The Reproductive Capacity of Plants. Bell, London.

Schaal, B.A. 1980. Reproductive capacity and seed size in *Lupinus texensis* . Amer. J. Bot. 67: 703-709.

Schaffer, W.M. 1974. Optimal reproductive effort in fluctuating environments. Amer. Nat. 103: 703-790.

Sokal, R.R., and Rohlf, F.J. 1981. Biometry. 2nd ed. Freeman, San Francisco.

Tamn, C.O. 1956. Further observations on the survival and flowering of some perennial herbs I. Oikos 7: 273-292.

Turner, M.D., and Rabinowitz, D. 1983. Factors affecting frequency distributions of plant mass: The absence of dominance and suppression in competing monocultures of *Festuca paradoxa* . Ecology 64: 469-475.

Werner, P.A., and Caswell, H. 1977. Population growth rates and age *versus* stage distribution models for Teasel (*Dipsacus sylvestris* Huds.). Ecology 58: 1103-1111.

TABLE 1

UNIVARIATE STATISTICS FOR PLANT FECUNDITY IN ANNUALS AND PERENNIALS

TRAIT	ANNUALS			PERENNIALS			P
	mean	s.e.	n	mean	s.e.	n	
1. Mean fruit number per plant	28.5	1.20	50	30.2	1.26	40	>0.05
2. CV fruit number per plant	122.8	8.38	50	77.6	5.29	40	<0.001
3. Skewness fruit number per plant	4.1	0.46	37	1.8	0.18	15	<0.001

Figure 1. Frequency distribution of the coefficient of variation of fruit number in natural populations of herbaceous annuals (white bars) and perennials (black bars).

FIG. 1

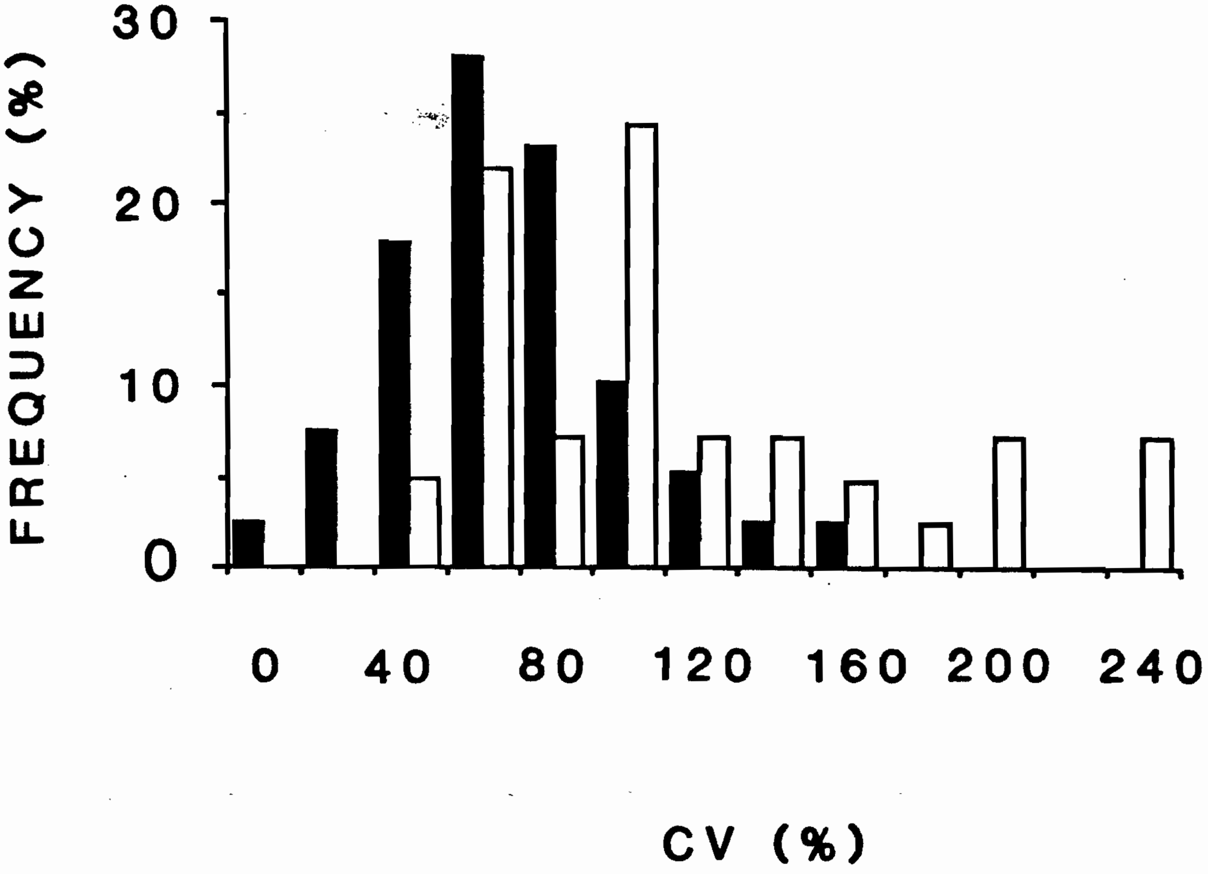


Figure 2. Frequency distribution of Skewness of fruit number in natural populations of herbaceous annuals (white bars) and perennials (black bars).

FIG.2

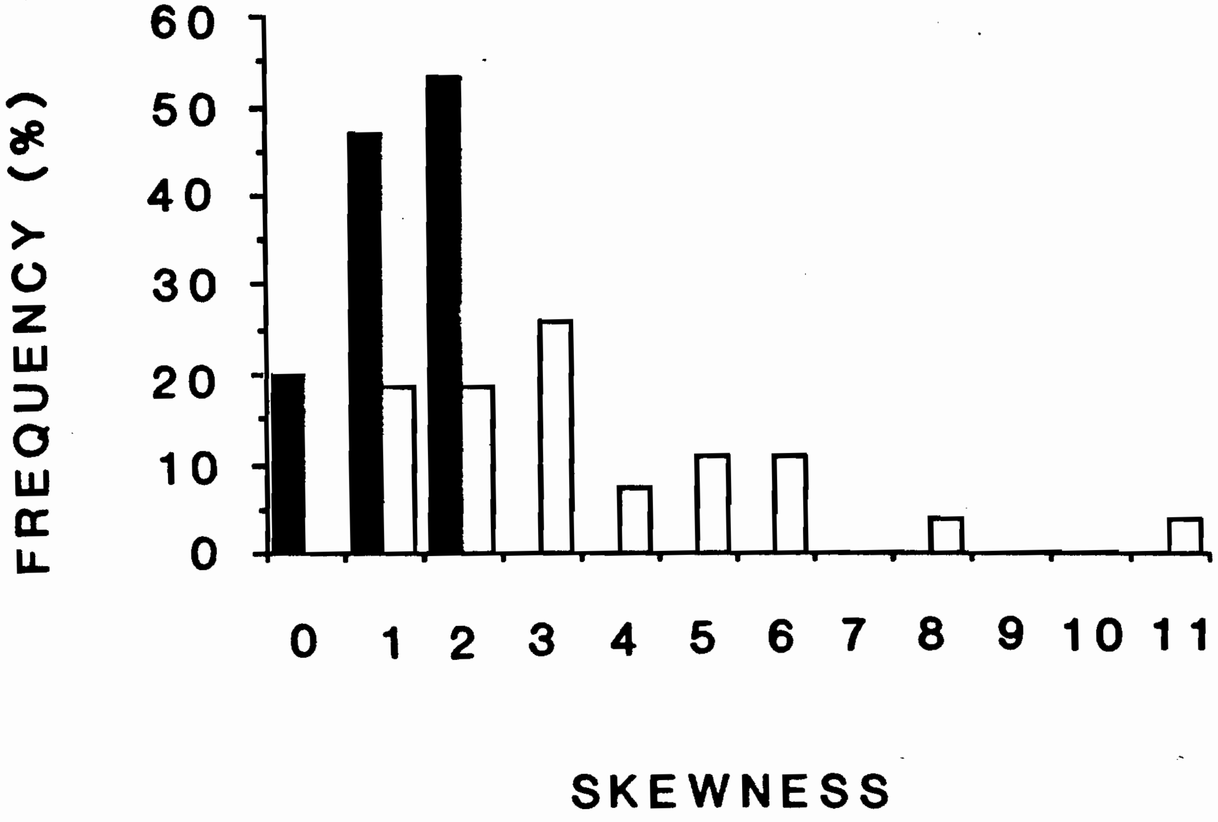
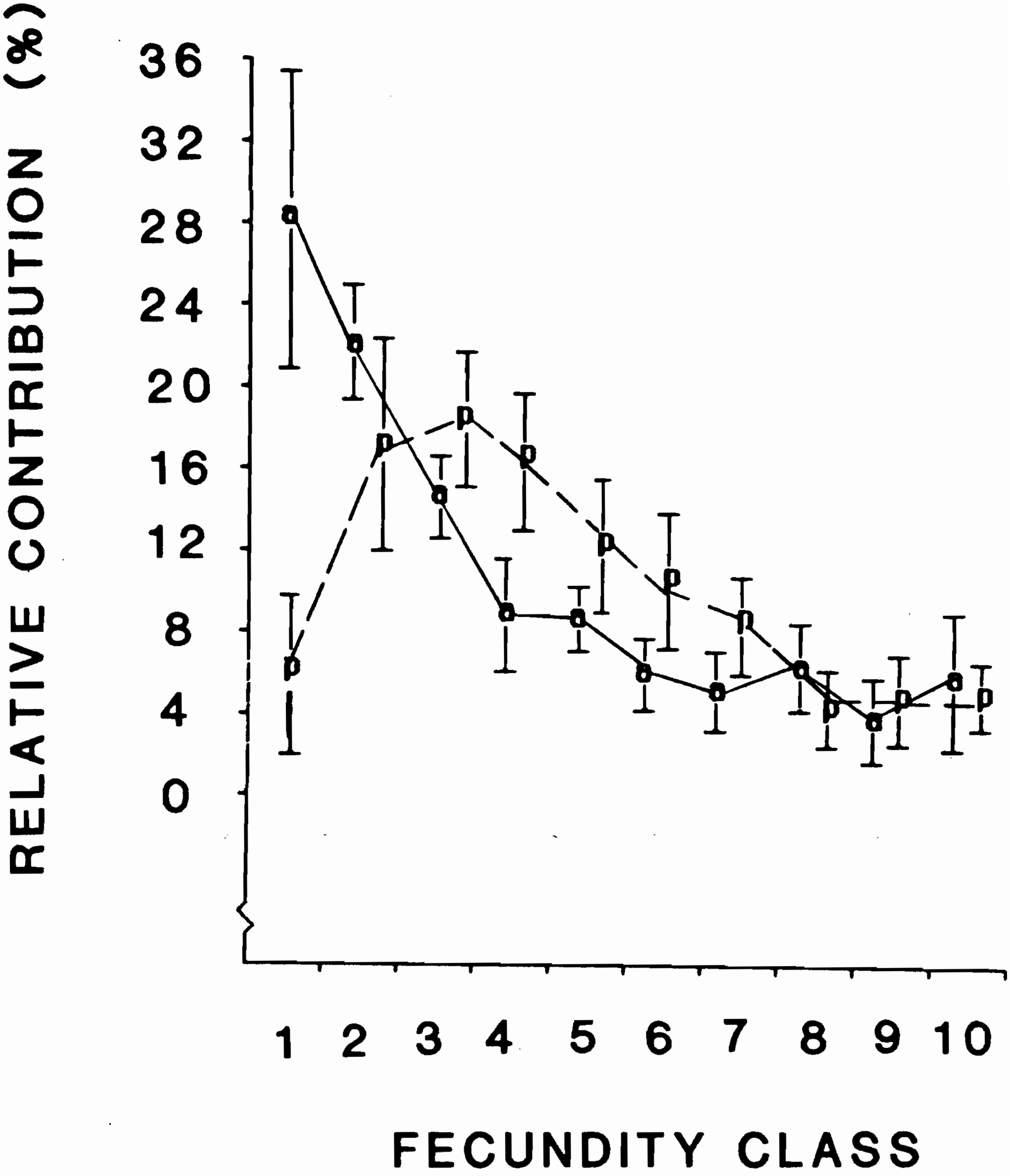


Figure 3. Mean (plus or minus 2 s.e.) relative contribution to the total population by individuals belonging to different fecundity classes in natural populations of herbaceous annuals and perennials.

FIG.3


RELATIVE CONTRIBUTION (%)
36
32
28
24
20
16
12
8
4
0
1
2
3
4
5
6
7
8
9
10
FECUNDITY CLASS
a
p

CONCLUSION

The first two chapters of the present thesis dealt with some methodological problems associated with the measurement of phenotypic variability. In Chapter 1, the relationship between two currently used statistical indexes of variation, the Gini Index (G) and the Coefficient of Variation (CV) was examined. It was shown through the use of hypothetical examples and real data sets that the two indexes are strongly correlated. G and CV are therefore two redundant measures of variability. The relative merits of the two indexes were discussed and it was concluded that the use of CV should be preferred over that of G in the comparative study of variability.

In Chapter 2, we dealt with some of the problems associated with the scaling of variability. Scaling is an important step in the study of variability since univariate statistics of dispersion, like the variance or the standard deviation, are often positively correlated with the mean. It is therefore necessary to statistically remove this effect in order to obtain unbiased (with respect to the mean) measurement of variability. Several statistical models are available to achieve this goal (least-squares regression, major axis, reduced major axis). We showed that of these three alternatives, only least-squares regression has the property that residual values (deviations from predicted values) are independent of the scaling variable (the x-variable which is the mean in our case). Thus it was concluded that least-squares regression should be used in scaling variation through analysis of residuals.

In the next three chapters, we presented a comparative study of the phenotypic variability in some morphometric and life history characters. In Chapter 3, we showed in a literature review that phenotypic variability as measured by CV is related to sexual size dimorphism in organisms as varied as insects, deer, and primates. Using literature data, a study of 279 bird species showed that males of species highly dimorphic tail length were more variable than those of species with little or no size dimorphism for this trait. This same effect was also found in females, though to a lesser degree. No such trends were found in a trait reaching less extreme degrees of sexual dimorphism, wing length. These results suggested that morphometric traits under sexual selection often exhibit high degrees of phenotypic variability. We suggested that, at least in some cases, such high variability might have its origin in positive allometric relationships between secondary sexual characters and body size.

In chapter 4, we studied the phenotypic variability of fecundity in natural populations of herbaceous plants, crustaceans, amphibians, reptiles, birds, and mammals. The following conclusions emerged from this literature survey. First, in all these taxonomic groups, with the possible exception of the crustaceans, CV of fecundity was independent of mean fecundity. Secondly, CV was greater and smaller in plants and birds respectively than in the other four groups. Finally, the variability of fecundity dependend on the age of measurement in both birds and plants, with CV increasing systematically from early to later developmental stages. In birds, CV of fledging production per nest was three times larger than CV of clutch size at laying; it was shown how this effect might be explained by the effect of moderate levels of stochastic variation in survival rates.

In chapter 5, we sought to relate phenotypic variability of fecundity in herbaceous plants to life history (annual *vs* perennial). An analysis of literature and original data showed that CV of fecundity (fruit number per plant) was significantly higher in annuals than in perennials. Mean fecundity however did not differ significantly among the two groups. This result was interpreted as a response to the combination of semelparity and constrained life span in annuals as opposed to perennials which are iteroparous and can have more variable life spans. It also suggests that phenotypic variability might be an important correlate of life history strategies.

Lastly, the following general conclusions can be drawn from the present study:

Phenotypic variability varies substantially among and within taxonomic groups, as well as among traits. Thus, comparisons of CVs across these levels should be made with caution, especially in the absence of *a priori* expectations. Empirical studies of variability can reveal patterns that are easily overlooked by more deterministic approaches. For example, we showed that sexually dimorphic traits differed between the two sexes not only in mean values, but also in their degree of variability. A comparison of the phenotypic variability of fecundity in annual and perennial plants also revealed that while no difference in mean fecundity among these two groups could be detected, they clearly differed in phenotypic variability. Empirical studies of phenotypic variability can also served as yardstick in future research in the sense that they provide an *a priori* expectation concerning the variability that should be observed in a particular taxonomic group or in a certain character.