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Meta-Analysis**



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*Ecology*, Vol. 73, No. 5 (Oct., 1992), 1699-1705.

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## LACK'S CLUTCH SIZE HYPOTHESIS: AN EXAMINATION OF THE EVIDENCE USING META-ANALYSIS<sup>1</sup>

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**Abstract.** Meta-analysis is a method ecologists may find useful for quantitatively reviewing and systematically examining results from a large number of studies on a subject for which there is conflicting evidence. I used meta-analysis to integrate results from 42 independent brood-enlargement studies and tested Lack's hypothesis that clutch size in birds has evolved toward that which produces the most surviving offspring. Cumulative evidence did not support Lack's hypothesis. Significantly (two-tailed  $P = .016$ ) more fledglings were produced in enlarged broods than in normal-sized broods, indicating parents could raise more young than they had eggs. The standardized treatment effect of brood enlargement across all studies was a mean ( $\pm 1$  SE) increase of 0.55 ( $\pm 0.22$ ) standard deviations in the number of young produced. This result does not appear to be affected by a publishing bias and is unlikely to be reversed by inclusion of additional studies. I also examined differences in methodology and species studied as possible confounding factors and explanations for conflicting results. Longer studies and species with altricial young were more likely to show food limitation. Latitude and date of study, degree of brood enlargement, validity of a study, and annual adult survival did not affect results.

**Key words:** brood enlargement; clutch size; factors affecting results of conflicting studies; food limitation; Lack's hypothesis; meta-analysis; quantitative review.

### INTRODUCTION

Lack (1947, 1948) hypothesized that natural selection has caused clutch size in birds to evolve toward that which produces the most surviving offspring. He further argued that the mechanism determining the upper limit to clutch size is parental ability to provide food for nestlings (Lack 1954, 1966). Numerous studies have tested this hypothesis by experimentally enlarging brood size. If parents of enlarged broods can produce significantly more offspring than parents of natural-sized broods, Lack's food limitation hypothesis is not supported.

Results of these brood size manipulation experiments have been conflicting, with researchers finding significant evidence for and against Lack's hypothesis. Several alternative hypotheses to food limitation have been proposed, including individual optima (Högstedt 1980), costs to parents (Nur 1988), nest size (Slagsvold 1982a), predation (Slagsvold 1982b, Lima 1987), incubation capacity (Hills 1980), a bad-years effect (Boyce and Perrins 1987), and nutritional constraints on female during laying (Slagsvold and Lifjeld 1988). Several qualitative reviews have shown that in the majority of cases parents can raise enlarged broods, but also that none of the alternative hypotheses provide a satisfactory explanation in all cases (Klomp 1970, Lessells 1986, Martin 1987, Ydenberg and Bertram 1989).

However, in a qualitative review one is limited to tallying of positive and negative results, with no allow-

ance for the probability associated with each result. Furthermore, when reviewing a subject on which there have been a large number of studies, such as Lack's hypothesis, it is impractical to use qualitative techniques to systematically examine differences in methodology and species studied as possible confounding factors and explanations for conflicting results. Such a large data set often forces selective inclusion or subjective weighting of studies in a qualitative review.

Meta-analysis is a method of integrating statistical results from independent studies (Glass 1976). It provides both a rigorous, quantitative analysis of cumulative evidence and a practical method of systematically and objectively examining a large data set for possible mediating variables. Meta-analysis frequently is used in psychology and medicine (Mann 1990), but rarely has been applied in ecology (Järvinen 1991).

In this study I used meta-analysis to combine results from independent brood enlargement experiments and tested Lack's food limitation hypothesis using the cumulative data set. I also recorded information on methodology and species studied to search for confounding factors that might help explain conflicting results and shed light on alternative hypotheses.

### METHODS

#### *Location and criteria for inclusion of studies*

I attempted to locate all published and unpublished studies in which brood size was experimentally enlarged by searching ornithological and ecological literature, *Biological Abstracts*, *Dissertation Abstracts International*, and abstracts from professional meetings.

<sup>1</sup> Manuscript received 1 March 1991; revised 21 November 1991; accepted 22 November 1991.

I did not use non-manipulative studies because they cannot separate effects of confounding factors such as variation in parental ability or territory quality. I found 77 studies ranging in date from 1954 through 1991 that could potentially have been included in the meta-analysis.

Each study had to meet the following criteria for inclusion: (1) the study was done on a wild population, not on captive birds or those supplied with unlimited food; (2) brood enlargements were successful, i.e., the foster chicks were accepted and cared for by the parents; (3) brood sizes were not altered subsequent to the initial enlargement; (4) data or analyses were not superseded by later studies on the same population; and (5) the method of brood enlargement and format of data presentation must allow examination of treatment (control or enlarged) effect—studies that randomly assigned brood size to nests without reporting the number of chicks originally present did not allow such a comparison (e.g., Crossner 1977, Nur 1984, Lessells 1986).

If a study met all the above requirements but reported insufficient data to allow calculations, I wrote the author requesting additional information. I was able to obtain sufficient information on 42 studies.

#### *Meta-analytic techniques*

It would not be meaningful to combine the absolute numbers of young raised by different species of birds or by different populations of a species because their clutch sizes may be different and may be the result of different sets of selective forces and constraints. Therefore, I converted the results of each study to a standardized measure of the effect of the brood enlargement treatment. This standardized treatment effect is the "effect size,"  $d$  (Cohen 1988), sometimes also called the "standardized difference between means" (Hedges and Olkin 1985) or the "standardized selection differential" (Endler 1986), and is calculated by:

$$d = (\bar{X}_e - \bar{X}_c) / SD,$$

where  $\bar{X}_e$  and  $\bar{X}_c$  are the mean numbers of young produced in experimental and control groups, respectively, and  $SD$  is the pooled standard deviation from both groups. Thus  $d$  is a measure in standard deviations of the difference in number of young produced in enlarged and control broods. I tested whether the mean effect size over all 42 studies was more different from zero than could be expected from chance alone.

Choice of which variance to use in calculating effect size is very important and can greatly affect results (Glass et al. 1981: 105–107), but authors disagree on whether the control (Glass et al. 1981, Cooper 1989), experimental (Hunter and Schmidt 1990), or pooled variance (Hedges and Olkin 1985) should be used. I compared standard deviation estimates from control and enlarged groups to judge whether pooling was appropriate. In 28 of 33 studies reporting both control and enlarged variances it was appropriate to use the

pooled variance, and in 5 cases it was not appropriate, in which case I used the control variance.

Some authors did not report group means or standard deviations, but presented results of tests on the differences between control and enlarged groups ( $n = 9$ ). In these cases I converted the statistic or  $P$  value from the test performed into the corresponding  $t$  statistic with appropriate degrees of freedom and calculated an estimate of effect size provided by Glass et al. (1981):

$$d = t(1/n_c + 1/n_e)^{0.5},$$

where  $t$  is Student's  $t$  statistic and  $n_e$  and  $n_c$  are the enlarged and control sample sizes.

I should point out that when conducting a meta-analysis it is desirable to use original data or complete summary statistics from each study, and I attempted to do so whenever possible. Estimating effect size from  $P$  values, as I was forced to do in a few cases, may introduce an additional source of error. In order to determine if I might have unwittingly added such an error, I used method of effect-size calculation as an independent variable in analyses of variation in effect sizes.

If the results of a study showed that control and experimental groups produced significantly different numbers of offspring, but the author reported only the critical probability (e.g.,  $P < .05$ ), I used the critical value and converted it as above ( $n = 5$ ). This resulted in a conservative measure of effect size because the actual  $P$  value was lower.

One study reported the number of offspring produced in experimental broods only, but this value was larger than the maximum possible number of offspring produced in control broods. In this case I used the maximum possible value for control broods, which minimized effect size and gave conservative results.

Authors of some studies presented separate results from different years or from different enlarged brood sizes. If the format of data allowed, I pooled data from all years or enlarged brood sizes to obtain one measure from each study ( $n = 5$ ). Including multiple results from a single study would violate assumptions of independence, inflate sample sizes used in statistical tests, and increase the probability of type-I error (Wolf 1986). If data from separate enlarged brood sizes were presented in such a way that they could not be pooled ( $n = 4$  studies), I used only data from the smallest enlarged size. This minimized the difference between control and enlarged groups, regardless of which produced more offspring, and gave a conservative result.

#### *Criticisms and biases of meta-analysis*

A common criticism of meta-analysis is that it is not possible to make valid inferences from an integration of studies that have diverse methods of measurement and that were done on different subjects (Glass et al. 1981). In other words, meta-analysis tries to compare

"apples and oranges." One method of dealing with such possible inconsistencies is to code aspects of the methodology and study species that might affect the results and make integration inappropriate and test them as potential mediating variables of effect size (Wolf 1986). I coded various aspects of each study that might lead to difficulties in integration: date of study (before 1970, 1970s, and 1980 or after); study length in number of nesting seasons; experimental sample size; degree of brood enlargement; latitude of study; development of young in study species (precocial, semiprecocial, semi-altricial, and altricial—see Ehrlich et al. 1988 for definitions; O'Connor 1984, Ricklefs 1984); and annual adult survival rate. Estimates of annual adult survival were obtained from the original study population ( $n = 19$ ), another population of the same species ( $n = 9$ ), or a closely related species ( $n = 14$ ), and were taken for some species from Lack (1954), Nelson (1979), Perrins and Birkhead (1983), and Newton (1989). I investigated the importance of these factors in explaining the variance in effect sizes by using them as independent variables in a multiple least-squares regression of effect sizes.

A related problem is that meta-analysis lumps results from studies with high and low validity. I coded both internal validity, based on aspects of methodology that might make results suspect, and external validity, ability to generalize results beyond the study, as either high or low. I gave a study low internal validity if: (1) control and enlarged broods consistently differed in some way, such as location within a colony, time of year, or age of parents, and this difference could not be corrected for; (2) manipulations disrupted natural patterns of hatching synchrony; or (3) foster chicks had a lower fledging rate than original chicks in the same nest. I gave a study low external validity if: (1) the study population might have been growing in response to a recent increase in food supply (see Ydenberg and Bertram 1989); or (2) the study population had experienced some recent form of selection of clutch size, such as egg collection by humans, that suggested the present clutch size might not be the result of long-term natural selection. I included validity as a potential mediating variable of effect size in the least-squares regression.

Another potential bias of meta-analysis, and the one most difficult to assess, is the possibility that published studies are a biased subset of all studies on a subject (Hunter and Schmidt 1990). This potential bias has been called the "file drawer problem" (Rosenthal 1979) because nonsignificant results may be more likely to be put in a researcher's file drawer and not published. This publishing bias can increase the probability of type-I error in a meta-analysis (Wolf 1986).

I attempted to determine if the data set I used might be affected by a publishing bias by conducting tests of independence using all 77 available studies. I tested if published studies were different in direction of results (supporting or not supporting Lack's hypothesis) from

unpublished studies, and also if the 42 studies I used were biased compared to all 77 available studies.

I also attempted to determine how likely it might be that results of the meta-analysis could be changed by inclusion of additional studies by calculating a "fail-safe ( $f_s$ ) sample size," the number of additional studies with zero net effect required to reduce the mean effect size ( $d$ ) to a minimum meaningful value ( $d_c$ ) (Hunter and Schmidt 1990):

$$N_{fs} = N(d/d_c - 1),$$

where  $N$  is the number of studies already used in the meta-analysis. Cohen (1988) suggests that as a general rule  $d = 0.2$  is a small effect,  $d = 0.5$  a moderate effect, and  $d = 0.8$  a large effect. Therefore, I calculated the number of additional studies with no net effect required to reduce the observed mean effect size to 0.2. It should be emphasized that this is the number of additional studies summing to exactly null results, i.e., whose  $d$ s sum to zero. It is possible that unlocated or unusable studies have a cumulative non-zero effect opposite to or in agreement with that found in the analysis.

## RESULTS

The standardized treatment effect across all studies was a mean ( $\pm 1$  SE) increase of 0.55 ( $\pm 0.22$ ) standard deviations in the number of young produced, which is significantly greater than zero ( $n = 42$ ,  $t = 2.52$ , two-tailed  $P = .016$ ), indicating enlarged broods produced more offspring than control broods (Table 1). The fail-safe sample size required to reduce the mean standardized treatment effect to 0.2 (regarded as a small effect) is 74 additional studies.

Results of least-squares regression of effect sizes on study characteristics that might act as mediating variables are shown in Table 2 ( $n = 42$ , overall  $R^2 = 0.434$ ). Only length of study and development of young were significant predictors of effect size. Other differences in methodology and species studied had no significant effects. I did a separate multiple regression of effect sizes adding degree of brood enlargement because two studies did not report this information and had to be omitted. Degree of brood enlargement did not significantly affect results ( $n = 40$ ,  $F = 0.13$ ,  $P = .73$ ). The addition of degree of brood enlargement to the regression did not qualitatively change the significance of original variables.

Tests of independence based on  $2 \times 2$  tables showed that there was no difference in direction of results in published vs. unpublished studies ( $\chi^2 = 0.001$ ,  $df = 1$ ,  $P = .97$ ) and also that the subset of 42 studies I used was not different in direction of results compared to all 77 available studies ( $\chi^2 = 0.049$ ,  $df = 1$ ,  $P = .82$ ).

## DISCUSSION

The food-limitation mechanism of Lack's clutch size hypothesis is not supported by cumulative evidence from 42 brood-enlargement studies. On average par-

TABLE 1. Summary of data and characteristics of each brood-enlargement study. Effect size,  $d$ , is a measure in standard deviations of the difference between the number of young produced from enlarged vs. control broods. Development code: 1 = precocial, 2 = semiprecocial, 3 = semialtricial, 4 = altricial.

Species	Effect size, $d$	Sample size (no. enlarged broods)	Study length (yr)	Lat. (°)	Control/enlarged brood size	Development	Adult survival	Reference*
<i>Diomedea immutabilis</i>	-1.14	18	1	28N	1/2	3	0.95	Rice and Kenyon 1962 <sup>b</sup>
<i>Puffinus puffinus</i>	2.53	42	1	51N	1/2	3	0.91	Perrins et al. 1973
<i>Oceanodroma furcata</i>	0.34	5	2	59N	1/2	3	0.85	Boersma et al. 1980
<i>Sula bassanus</i>	1.84	13	1	56N	1/2	4	0.94	Nelson 1964 <sup>d</sup>
<i>Sula capensis</i>	1.96	22	2	32S	1/2	4	0.94	Jarvis 1974 <sup>b</sup>
<i>Sula sula</i>	-0.92	3	1	1S	1/2	4	0.94	Nelson 1966
<i>Stercorarius longicaudus</i>	1.63	4	1	65N	2/3	2	0.88	Andersson 1976
<i>Larus argentatus</i>	3.73	5	1	43N	2.5/4.45	2	0.90	Haymes and Morris 1977 <sup>d</sup>
<i>Larus californicus</i>	1.14	22	1	38N	2/3	2	0.82	Winkler 1985 <sup>d</sup>
<i>Larus glaucescens</i>	0.33	88	1	49N	2.72/4.74	2	0.90	Vermeer 1963
<i>Creagrus furcatus</i>	0.89	30	2	1S	1/2	2	0.97	Harris 1970
<i>Calidris pusilla</i>	-3.22	27	2	71N	4/5	1	0.70	Safriel 1975
<i>Alca torda</i>	0.73	14	1	51N	1/2	2	0.89	Lloyd 1977 <sup>b,c</sup>
<i>Cephus grylle</i>	1.54	14	2	65N	2/3	2	0.87	Petersen 1981 <sup>b</sup>
<i>Fratercula arctica</i>	0.14	10	1	47N	1/2	2	0.95	Nettleship 1972
<i>Fratercula arctica</i>	1.72	4	1	51N	1/2	2	0.95	Corkhill 1973 <sup>b</sup>
<i>F. cirrhata</i> + <i>corniculata</i>	1.02	28	1	57N	1/2	2	0.95	Wehle 1983
<i>Necrosyrtes monachus</i>	1.73	3	1	13N	1/2	3	0.70	Mundy and Cook 1975 <sup>d,c</sup>
<i>Rostrhamus sociabilis</i>	0.00	7	2	8N	2/4	3	0.70	Beisinger 1990
<i>Buteogallus meridionalis</i>	-0.59	10	2	8N	1/2	3	0.71	Mader 1982 <sup>b</sup>
<i>Falco sparverius</i>	-0.36	10	2	45N	5/7	3	0.53	Gard and Bird 1990
<i>Aegolius funereus</i>	0.06	19	2	63N	5.81/7.07	3	0.65	Korpimäki 1988
<i>Aerodramus spodiopygius</i>	0.81	11	1	18S	2/3	4	0.80	Tarburton 1987 <sup>b</sup>
<i>Empidonax minimus</i>	3.82	14	1	50N	4/5	4	0.40	Briskie and Sealy 1989
<i>Tyrannus tyrannus</i>	-2.80	2	1	43N	4/5	4	0.45	Murphy 1983 <sup>b,c</sup>
<i>Tachycineta bicolor</i>	2.44	14	1	42N	6.3/8.4	4	0.39	DeSteven 1980
<i>Tachycineta bicolor</i>	0.92	8	1	50N	5.7/7.9	4	0.42	Wiggins 1990 <sup>b</sup>
<i>Tachycineta bicolor</i>	0.92	15	1	45N	5.3/7.3	4	0.35	Wheelwright et al. 1991 <sup>b</sup>
<i>Pica pica</i>	-1.34	5	3	57N	6.2/7.2	4	0.65	Högstedt 1980
<i>Corvus frugilegus</i>	1.67	18	1	63N	3.3/4.1	4	0.80	Røskaft 1985 <sup>c</sup>
<i>Corvus corone</i>	0.73	22	3	55N	4.28/5.59	4	0.80	Loman 1980
<i>Parus major</i>	-0.58	68	4	55N	8.84/13.5	4	0.38	Smith et al. 1989 <sup>a,b,c</sup>
<i>Parus montanus</i>	-0.20	20	2	65N	7.84/9.84	4	0.49	Orell and Koivula 1988 <sup>a,b</sup>
<i>Troglodytes aedon</i>	0.15	37	3	40N	7/8	4	0.40	Finke et al. 1987
<i>Ficedula hypoleuca</i>	-0.40	81	2	60N	...	4	0.40	Alatalo and Lundberg 1989 <sup>a,b</sup>
<i>Ficedula hypoleuca</i>	-0.18	24	2	57N	...	4	0.40	Askenmo 1977 <sup>b,c</sup>
<i>Ficedula albicollis</i>	-1.00	57	3	58N	6/7	4	0.41	Gustafsson and Sutherland 1988 <sup>a,b,c</sup>
<i>Turdus pilaris</i>	0.58	57	3	63N	5.5/7	4	0.60	Slagsvold 1982 <sup>a</sup>
<i>Agelaius phoeniceus</i>	1.19	17	1	42N	3.5/5.5	4	0.75	Cronmiller and Thompson 1980 <sup>b</sup>
<i>Quelea quelea</i>	-0.34	6	1	14N	3/4.5	4	0.44	Ward 1965
<i>Passer domesticus</i>	-0.24	14	1	51N	4.25/5.29	4	0.50	Schifferli 1978 <sup>b</sup>
<i>Passer domesticus</i>	0.73	8	1	42N	3.7/6.3	4	0.50	Hegner and Wingfield 1987 <sup>a,b,c</sup>

\* Superscripts following reference entries have the following meaning: <sup>a</sup> = Effect size based on number of recruits or offspring surviving to following year; <sup>b</sup> = Fledglings from enlarged broods smaller than those from control broods; <sup>c</sup> = Brood enlargement had some detrimental effect on parents; <sup>d</sup> or <sup>e</sup> = Study had low external or internal validity, respectively. For definitions, see *Methods: Criticisms and biases of meta-analysis*.

ents were able to raise significantly more young than the number of eggs they laid. This confirmed the findings of previous qualitative reviews (Lessells 1986, Martin 1987, Ydenberg and Bertram 1989). Moreover, this study provides a quantitative measure of the evidence for Lack's hypothesis, and the low  $P$  value as-

sociated with the cumulative  $t$  test allows statistical rejection of the food limitation mechanism.

The large fail-safe  $N$  of 74 more studies indicates these results are robust. The subset of studies I was able to use was not biased in direction of results, nor did the data set appear to be affected by a publishing

bias. It seems unlikely that inclusion of additional studies would greatly affect results of this meta-analysis, unless a large number of unlocated studies exist that exhibit a cumulative net effect opposite to that in the 77 studies I found.

Multiple regression of effect sizes showed that the length of a study significantly affected results (Table 2). Studies longer than one year were more likely to show that parents could not raise enlarged broods (Table 1,  $\chi^2 = 3.94$ ,  $df = 1$ ,  $P = .047$ ). This suggests that clutch size is optimized over a period  $> 1$  yr and reflects between-year variation. These results support the bad-years effect proposed by Boyce and Perrins (1987) in which larger clutches experience disproportionate mortality in bad years, favoring an intermediate clutch size in all years combined. Bad years may occur infrequently, and they would be detected by 1-yr studies in a fraction inversely proportional to their interval of occurrence.

Other differences in methodology, including experimental sample size, date of study, and degree of brood enlargement, had no systematic effect. These factors did not cause problems with integration of results into a single meta-analysis.

Validity of study was not a significant factor in explaining variation in effect sizes (Table 2). This does not imply that the validity of a particular study did not affect its results. It indicates there was no systematic effect of validity on the overall results caused by the distribution of studies with high and low validity.

The method of effect-size calculation did not systematically affect results. I did not introduce a significant error by using  $P$  values to estimate effect size.

Clutch size in birds often increases with latitude, both intraspecifically and interspecifically (Lack 1947, 1948, 1968, Skutch 1949). These trends may reflect differences in seasonal food abundance and a corresponding ability of parents to provision nestlings, but it has been argued that tropical birds are not food limited (Skutch 1949, 1985). I found that the ability of parents to raise enlarged broods was not affected by latitude, and thus that importance of food limitation on clutch size does not change with latitude.

Lack's hypothesis was originally proposed to explain evolution of clutch size in birds that feed their young (Lack 1947, 1948). It has since been extended to species that do not feed their young by using mechanisms involving other forms of parental care, such as defense against predators (Safriel 1975, Lessells 1986). It is not surprising that there were differences among categories of development of young in the ability of parents to raise enlarged broods. Altricial species were less likely to raise enlarged broods, reflecting their faster growth rates and the greater demands placed on parents during the nestling stage. Precocial species were more often able to raise enlarged broods, suggesting their clutch sizes were more limited by other mechanisms (see Winkler and Walters 1983).

TABLE 2. Results of least squares regression of effect sizes on study aspects as potential confounding variables. For definitions see *Methods: Meta-analytic techniques and Criticisms and biases of meta-analysis*.

Variable	$F$	Two-tailed $P$
Study length	4.74	0.037
Experimental sample size	0.11	0.75
Date of study	1.97	0.16
Validity	0.84	0.37
Latitude	0.31	0.58
Precociality of young	3.29	0.034
Adult survival	1.18	0.29
Method of effect-size calculation	0.17	0.69

The number of young raised in one or even a few years may be only a partial measure of lifetime fitness. A more complete measure includes costs of reproduction to parents and effect on adult survival and ability to reproduce in subsequent years (Williams 1966, Klomp 1970, Högstedt 1981, Nur 1988). If the increased costs to parents of raising enlarged broods decreases future reproductive output, it follows that long-lived species should be less likely to raise enlarged broods because their potential loss could be greater (Charnov and Krebs 1974). However, I found that annual adult survival did not affect the outcome of brood enlargements. Long-lived species were just as likely to raise enlarged broods.

Some of the conflicting results obtained in brood-enlargement studies may be caused by differences in definitions of productivity (Martin 1987). Some studies compared the numbers of fledglings produced in normal-sized and enlarged broods, while others compared the numbers of offspring that survived and were recruited into the breeding population. Optimum clutch size may reflect a trade-off between quality and quantity of offspring (Nur 1984, Smith et al. 1989). Some authors attempted to infer survival based on minimum fledging mass, although it is not clear if fledging mass is always a good indicator of future survival (Lack 1966, Schifferli 1978, Garnett 1981, Nur 1984, but see Perrins et al. 1973). Clearly, it is most accurate to use numbers of recruits for comparison, but such data is difficult to obtain and may not be feasible in species with low site fidelity. Only 5 of the 42 studies used in the meta-analysis provided information on the number of recruits (Table 1). In contrast to the pattern observed in all 42 studies, 4 of these 5 supported Lack's hypothesis. However, these results may be confounded by length of study and phylogeny, and should be interpreted with caution; four out of five were longer than 1 yr and four were on two pairs of closely related species.

In summary, I found that the food-limitation mechanism of Lack's clutch size hypothesis can be statistically rejected based on cumulative results of 42 brood-enlargement studies. This study was not affected by a publishing bias or by studies with small sample size or

low validity, and it is unlikely that the results would be changed by inclusion of additional studies. The length of a study and degree of development of young significantly affected results, indicating that yearly variation is important in the evolution of clutch size and that altricial species are more food-limited than precocial species. Birds breeding at different latitudes are equally affected by food limitation. Despite theoretical differences in the effect of annual adult survival on lifetime fitness, long-lived species were just as likely to increase reproductive effort to raise enlarged broods.

This study demonstrates how meta-analysis can be used to integrate results from a large number of studies. It allows quantitative evaluation of evidence and provides insight on differences among studies and alternative explanations. The field of ecology has grown rapidly, and the number of experimental studies is increasing particularly quickly. For a number of topics the point has been reached where a synthesis of existing knowledge would be useful. Meta-analysis provides an objective method of quantitatively reviewing and systematically examining information.

#### ACKNOWLEDGMENTS

This study originated as a term project I did for Doug Levey's fall 1990 avian biology class at the University of Florida. I thank Doug for suggesting the idea of a meta-analysis of Lack's hypothesis and for encouraging me to pursue it beyond the class. I gratefully acknowledge Sten Asbirk, Diane DeSteven, Nicholas Gard, Michael P. Harris, J. B. Nelson, Henrik G. Smith, Nat Wheelwright, and David Wiggins for sending me unpublished data or a manuscript, and Steve Beisinger, Kate Lessells, Spencer G. Sealy, and Ron Ydenberg for their correspondence. Without the additional information supplied by these people this study would not have been possible. Ken Burnham and Doug Levey provided many helpful criticisms that greatly improved the manuscript. Grace Kiltie helped prepare the manuscript.

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