

## Life histories of birds: clutch size, longevity, and body mass among North American game birds

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Clutch size, longevity, and body mass data for 54 North American game birds were extracted from the literature to test the hypothesis that a trade-off exists between fecundity and survival among avian species. Species with larger clutch sizes live shorter lives than species with smaller clutch sizes ( $r = -0.38$ ,  $n = 54$ ,  $P < 0.01$ ). This relationship still holds when the effects of body mass are removed ( $r = -0.34$ , 51 df,  $P < 0.05$ ), indicating that the relationship is not simply a function of body mass. This latter finding is inconsistent with previous life-history studies, perhaps because previous researchers did not attempt to remove body mass effects from their life-history investigations. Results are similar ( $P < 0.05$ ) when mean values of life-history traits are examined at the generic level. However, no relationships ( $P > 0.05$ ) among mean values of life-history traits occur at any taxonomic level higher than genus or when species are grouped with respect to feeding habits. This might be the result of low sample size. I conclude that the evolution of clutch size is influenced by longevity, or vice versa, among species and genera of North American game birds.

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Des données sur 54 espèces nord-américaines de gibier à plume ont été repérées dans la littérature (nombre d'oeufs par couvée, longévité et masse totale) afin de vérifier l'hypothèse selon laquelle il s'établit un équilibre entre la fécondité et la survie chez les oiseaux. Les espèces qui pondent plus de petits ont une durée de vie plus courte que les espèces qui pondent moins d'oeufs ( $r = -0,38$ ,  $n = 54$ ,  $P < 0,01$ ). Cette affirmation reste vraie lorsque les effets de la masse totale sont éliminés ( $r = -0,34$ , 51 dl,  $P < 0,05$ ), ce qui démontre que cette relation n'est pas seulement une fonction de la masse totale. Cette conclusion vient à l'encontre des études antérieures sur le développement, peut-être parce que les chercheurs n'ont pas éliminé les effets de la masse du corps au cours de leurs investigations. Les résultats sont semblables ( $P < 0,05$ ) lorsque les valeurs moyennes des paramètres du développement sont examinés au niveau générique. Cependant, il n'y a pas de relation ( $P > 0,05$ ) entre les valeurs moyennes de ces paramètres à des niveaux taxonomiques supérieurs au niveau générique ou lorsque les espèces sont regroupées en fonction de leurs habitudes alimentaires. Il faut peut-être reconnaître là l'effet de la taille trop faible de l'échantillon. Je conclus que l'évolution du nombre d'oeufs par couvée est influencée par la longévité, ou vice versa, chez les espèces ou les genres nord-américains de gibier à plume.

[Traduit par la revue]

### Introduction

Theoretical arguments suggest that costs of reproduction, such as the amount of energy used, predation risks, exposure to elements, and accidents (see Ricklefs 1974), should adversely affect survival rates in animals (Cody 1966; Williams 1966; Charnov and Krebs 1974; Stearns 1976; Bell 1980, 1984a, 1984b). For example, clutch size is a major cost in reproduction, so it should inversely covary with longevity in birds (Haukioja and Hakala 1979; Stenseth 1984; Reznick 1985). However, empirical studies of birds have not always provided convincing evidence of this relationship. Some intraspecific studies have supported the expected inverse relationship between reproduction and survival (Goodman 1974; Askenmo 1979; Bryant 1979; Nur 1984; Ekman and Askenmo 1986), whereas others have indicated either a positive or no relationship between these traits (De Steven 1980; Hogstedt 1981; Smith 1981; Roskaft 1985). Interspecific studies of mammals have supported the predicted inverse relationship between litter size and survival (Tuomi 1980; Millar and Zammuto 1983), whereas interspecific studies of birds on the subject are lacking.

Life-history studies of birds and mammals indicate that longevity, clutch size, and litter size correlate highly with body mass (Sacher 1959; Lindstedt and Calder 1976, 1981; Blueweiss et al. 1978; Western 1979; Tuomi 1980; Cabana et al. 1982; Western and Ssemakula 1982; Millar and Zammuto 1983; Calder 1984). Body mass has been proposed to be the underlying variable causing the relationships observed among many life-history

traits (Western and Ssemakula 1982; Peters 1983; Calder 1984; Lindstedt et al. 1986). However, recent evidence from partial correlations suggests that the relationship between age at maturity and longevity may not depend upon body mass within and among species of mammals (Harvey and Zammuto 1985). This raises the possibility that relationships observed among life-history traits of birds do not depend solely upon body mass either.

My purpose was to examine the relationship between clutch size and longevity, and to determine its dependency upon body mass among North American game birds. An inverse correlation ( $P < 0.05$ ) between clutch size and longevity, corrected for body mass effects, would be consistent with the fecundity-survival trade-off hypothesis and the balanced mortality hypothesis (see Price 1974; Bell 1984a). These hypotheses propose that either high fecundity accompanies low survival or low fecundity accompanies high survival because costs of reproduction are manifested as reduced survival in animals. Game birds were chosen for examination because large accurate samples of mean clutch sizes and longevities are available. Too few data are available for a comparable study on nongame birds (see sample sizes of Clapp et al. 1982, Clapp et al. 1983; Klimkiewicz et al. 1983; compare changes with Kennard 1975).

### Methods

Clutch size as completed clutches, longevity derived from banding records or life tables, and body mass of adult females were extracted

TABLE 1. Clutch size, longevity, body mass, and ecological categories for 36 North American waterfowl

	Mean clutch size (n) <sup>a</sup>	Longevity <sup>b</sup> (years)	Female body mass <sup>c</sup> (g)	Ecological category <sup>d</sup>	References <sup>e</sup>
Fulvous Whistling-Duck ( <i>Dendrocygna bicolor</i> )	9.6 (17)	6.5	710	1	1,2
Black-bellied Whistling-Duck ( <i>Dendrocygna autumnalis</i> )	13.4 (778)	8.2	849	1	3
Greater White-fronted Goose ( <i>Anser albifrons</i> )	4.7 (378)	20.3	2587	1	2,4,5
Snow Goose ( <i>Chen caerulescens</i> )	3.6 (1196)	26.6	2540 <sup>f</sup>	1	6-8
Ross' Goose ( <i>Chen rossii</i> )	3.6 (906)	19.6	1588	1	9
Emperor Goose ( <i>Chen canagica</i> )	4.8 (791)	6.3	2750	1	4,10
Brant ( <i>Branta bernicla</i> )	3.6 (2860)	19.6	1230	1	2,4,11
Canada Goose ( <i>Branta canadensis</i> )	4.7 (17 295) <sup>g</sup>	23.5	3033 <sup>f</sup>	1	4,8,12-29
Wood Duck ( <i>Aix sponsa</i> )	12.7 (2844)	17.6	635	2	2,8,29-36
Green-winged Teal ( <i>Anas crecca</i> )	8.7 (126)	20.3	318	2	2,8,37,38
American Black Duck ( <i>Anas rubripes</i> )	9.3 (1182)	26.4	1100	2	2,8,29,39,40
Mottled Duck ( <i>Anas fulvigula</i> )	9.9 (1467)	13.4	968	2	2,29,41,42
Mallard ( <i>Anas platyrhynchos</i> )	8.8 (1725)	23.4	1082	2	29,37,38,40,43-51
Northern Pintail ( <i>Anas acuta</i> )	7.7 (1668)	20.5	986	2	2,8,37,38,44,45,49,52
Blue-winged Teal ( <i>Anas discors</i> )	10.0 (3197)	17.4	363	2	8,29,37,38,47,52-59
Cinnamon Teal ( <i>Anas cyanoptera</i> )	8.7 (1928)	12.9	363	2	2,29,44,45,47,49,60
Northern Shoveler ( <i>Anas clypeata</i> )	9.4 (861)	16.6	590	2	2,8,37,38,44,45,47,49
Gadwall ( <i>Anas strepera</i> )	9.9 (4168)	17.7	849	2	2,8,37,38,42,44,45,49,53,85
American Wigeon ( <i>Anas americana</i> )	8.9 (144)	21.3	719	2	2,8,37,38,47
Canvasback ( <i>Aythya valisineria</i> )	7.5 (2193)	18.8	1190	3	2,37,58,61-63
Redhead ( <i>Aythya americana</i> )	10.6 (1772)	21.4	990	3	2,8,37,45,49,62,64,65
Ring-necked Duck ( <i>Aythya collaris</i> )	9.0 (487)	16.9	680	3	8,29,58,66
Greater Scaup ( <i>Aythya marila</i> )	9.6 (1551)	18.3	957	3	2,42,67
Lesser Scaup ( <i>Aythya affinis</i> )	9.2 (896)	18.3	790	3	2,8,37,45,58
Common Eider ( <i>Somateria mollissima</i> )	3.6 (9327)	14.8	1915	3	68-74
King Eider ( <i>Somateria spectabilis</i> )	4.9 (53)	18.9	1567	3	2,75
Steller's Eider ( <i>Polysticta stelleri</i> )	7.7 (10)	12.3	842	3	2,76,77
Oldsquaw ( <i>Ciangula hyemalis</i> )	7.5 (307)	15.3	814	3	2,29,42,78
White-winged Scoter ( <i>Melanitta fusca</i> )	8.8 (355)	15.5	1200	3	2,29,79,80,87
Common Goldeneye ( <i>Bucephala clangula</i> )	9.4 (148)	14.3	800	3	2,8,81,86
Barrow's Goldeneye ( <i>Bucephala islandica</i> )	10.2 (333)	15.3	730	3	2,42
Bufflehead ( <i>Bucephala albeola</i> )	8.8 (263)	12.5	334	3	82
Hooded Merganser ( <i>Lophodytes cucullatus</i> )	10.4 (218)	11.3	540	3	2,8,83

TABLE 1. (concluded)

	Mean clutch size (n) <sup>a</sup>	Longevity <sup>b</sup> (years)	Female body mass <sup>c</sup> (g)	Ecological category <sup>d</sup>	References <sup>e</sup>
Common Merganser ( <i>Mergus merganser</i> )	9.6 (87)	13.4	1232	3	8,29,79
Red-breasted Merganser ( <i>Mergus serrator</i> )	9.2 (342)	5.4	908	3	2,8,29,42,67,79
Ruddy Duck ( <i>Oxyura jamaicensis</i> )	7.9 (401)	13.6	499	3	2,8,37,44,45,49,64,65,84

<sup>a</sup>Weighted mean from listed references after adjustment for repeated data of review publications where possible. Sample size in parentheses.

<sup>b</sup>Longevity from banding records (Clapp et al. 1982; Clapp et al. 1983; Houston and Brown 1983).

<sup>c</sup>All body mass data were extracted from Dunning (1984). Some "female" masses are for both sexes combined where sexual dimorphism does not exist or study did not differentiate.

<sup>d</sup>Ecological category determined by feeding habits outlined in Martin et al. (1951): 1, geese; 2, puddle ducks; 3, diving ducks.

<sup>e</sup>References: 1, Cottam and Glazener 1959; 2, Bellrose 1976; 3, McCamant and Bolen 1979; 4, Mickelson 1975; 5, Lensink 1969; 6, Lemieux 1959; 7, Uspenskii 1965; 8, Peck and James 1983; 9, Ryder 1967; 10, Eisenhauer and Kirkpatrick 1977; 11, Barry 1962; 12, Steel et al. 1957; 13, Kossack 1950; 14, Williams and Marshall 1937; 15, Naylor 1953; 16, Miller and Collins 1953; 17, Naylor and Hunt 1954; 18, Geis 1956; 19, MacInnes et al. 1974; 20, Vermeer 1970; 21, Hanson and Eberhardt 1971; 22, Dow 1943; 23, Dimmick 1968; 24, Lebeda and Ratti 1983; 25, Raveling 1977; 26, Raveling 1979; 27, Cooper 1978; 28, Krohn and Bizeau 1980; 29, Schemnitz 1980; 30, Beshears 1974; 31, Lacaillade 1958; 32, Lee 1954; 33, Leopold 1951; 34, McLaughlin and Grice 1952; 35, Heusmann 1975; 36, Wenner and Marion 1981; 37, Keith 1961; 38, Duebbert and Lokemoen 1976; 39, Stotts and Davis 1960; 40, Coulter and Miller 1968; 41, Stieglitz and Wilson 1968; 42, Bengtson 1971; 43, Figley and Vandruuff 1982; 44, Hunt and Naylor 1955; 45, Miller and Collins 1954; 46, Dzubin and Gollop 1972; 47, Girard 1941; 48, Earl 1950; 49, Williams and Marshall 1938; 50, Anderson 1957; 51, Titman and Lowther 1975; 52, SOWLS 1955; 53, Martz 1967; 54, Lee et al. 1964; 55, Glover 1956; 56, Dane 1966; 57, Bennett 1938; 58, Townsend 1966; 59, Miller and Johnson 1978; 60, Spencer 1953; 61, Sugden 1978; 62, Bouffard 1983; 63, Stoult 1982; 64, Lokemoen 1966; 65, McKnight 1974; 66, Mendall 1958; 67, Weller et al. 1969; 68, Cooch 1965; 69, Freeman 1970; 70, Gross 1938; 71, Lewis 1939; 72, Paynter 1951; 73, Korschgen 1977; 74, Johnsgard 1973; 75, Hanson et al. 1956; 76, Bent 1925; 77, Brandt 1943; 78, Alison 1975; 79, Hilden 1964; 80, Brown and Brown 1981; 81, Moyle 1964; 82, Erskine 1972; 83, Morse et al. 1969; 84, Low 1941; 85, Duebbert 1966; 86, Grenquist 1963; 87, Houston and Brown 1983.

<sup>f</sup>Weighted mean among subspecies from Dunning (1984).

<sup>g</sup>Includes newly calculated weighted mean from Table 25 of Krohn and Bizeau (1980) without repeating data of references given in footnote e.

from the literature for 54 of the 70+ North American game birds (waterfowl, shore and upland species; see Tables 1 and 2). Body mass data of adult females were from Dunning (1984), whereas most longevity data were from Clapp and co-workers (Clapp et al. 1982; Clapp et al. 1983). Mean clutch size, weighted by the number of clutches per study, was calculated (Sokal and Rohlf 1981: p. 41) for each species using data from about 150 sources (see Tables 1 and 2).

Analyses that use data from many compiled sources may be biased by such factors as geographic or seasonal variation, effects of age or physical condition, reneesting attempts, or phenology. Several tests were made to consider some potential biases for each variable to allow a better understanding of the strengths and weaknesses of the data set used in the present study.

Body masses used in this study represent the largest sample available from single populations or studies, usually from North America (Dunning 1984). Brough (1983) used an average of nine worldwide sources for each species for his body mass estimates. Presumably, Brough's (1983) procedure should reduce directional biases towards larger or smaller masses that may be inherent in Dunning's (1984) procedure by averaging them over nine populations or studies. An *F*-test and a paired *t*-test were used to determine if there were any consistent biases towards larger or smaller female body masses in either Brough's (1983) or Dunning's (1984) studies.

Most longevity estimates used here are the current maximum ages reached by known-age banded members of each species (Clapp et al. 1982; Clapp et al. 1983). Mean longevity may be a more desirable measure of longevity since one individual may live longer than most members of that species by chance, causing an inflated longevity estimate for the species. However, mean longevity is available for fewer than five of the species discussed here and cannot be calculated from the published data. I examined the relationship between the current maximum and mean longevity in mammals using data from Jones (1982) and Millar and Zammuto (1983); current maximum longevity was highly correlated ( $P < 0.001$ ) with mean longevity. Additionally, other investigators have found theoretical and empirical support indicating that this relationship probably applies to other mammals and other animals (Zachmann and Logan 1984; Harvey and Clutton-Brock 1985), so the current maximum longevity should provide

the best available measure of longevity for these birds. Maximum longevity estimates should increase with time as the number of bandings and recaptures increase for a species and then they should become relatively stable once a large enough sample of each species has been banded and recaptured. An *F*-test and a paired *t*-test were used to determine if there were any consistent biases of longevity estimates between the studies of Kennard (1975) and Clapp and co-workers (Clapp et al. 1982; Clapp et al. 1983). Additionally, the relationship between longevity and clutch size was reexamined with partial correlation analysis, holding constant the effects of the number of recoveries (see Clapp et al. 1982; Clapp et al. 1983) for a species. This analysis ascertained if the relationship between clutch size and longevity was biased by either inflated longevity estimates caused by large sample sizes or by deflated longevity estimates caused by small sample sizes.

Mean clutch size estimates used in this study were calculated from many known clutch sizes for the 54 species from about 150 sources (see Tables 1 and 2). Reneesting attempts and the number of clutches per season could not be estimated because they are unknown for most species, so mean clutch size was weighted by the number of clutches per study (see Sokal and Rohlf 1981: p. 41) and was defined as the mean number of eggs per nest for each species. Further research may indicate better measures of reproductive effort for these birds but presently mean clutch size for a species should provide the best available index of reproductive costs for these birds (Reznick 1985). Unlike body mass and longevity data, no comparable studies collected clutch size data with the method used here and therefore comparisons with other studies cannot be made.

Distributions for clutch size, longevity, and body mass data were examined for normality with Kolmogorov-Smirnov one-sample tests among all species. The statistical relationships among the three life-history traits were examined among all species with simple, logistic (natural log), and (or) partial correlation analyses (Nie et al. 1975).

Large numbers of species within a genus (e.g., *Anas*) or ecological type (e.g., puddle ducks) may swamp results in interspecific studies so that resulting conclusions become biased towards characteristics of the over-represented genus or ecological type instead of being representative

TABLE 2. Clutch size, longevity, body mass, and ecological categories for 18 North American upland game and shore birds

	Mean clutch size (n) <sup>a</sup>	Longevity <sup>b</sup> (years)	Female body mass <sup>c</sup> (g)	Ecological category <sup>d</sup>	References <sup>e</sup>
Spruce Grouse ( <i>Dendragapus canadensis</i> )	6.1 (84)	5.3	456	4	1-3
Blue Grouse ( <i>Dendragapus obscurus</i> )	6.2 (221)	10.9	891	4	4-7
Ruffed Grouse ( <i>Bonasa umbellus</i> )	11.3 (1792)	7.6	532	4	3,8-10
Sharp-tailed Grouse ( <i>Tympanuchus phasianellus</i> )	11.3 (191)	6.3	817	4	10-13
Wild Turkey ( <i>Meleagris gallopavo</i> )	11.7 (152)	12.5	4222	4	10,14-17
Northern Bobwhite ( <i>Colinus virginianus</i> )	13.1 (1928)	6.4	178	4	3,10,18-26
Scaled Quail ( <i>Callipepla squamata</i> )	13.4 (81)	5.5 <sup>f</sup>	177	4	27,28
Gambel's Quail ( <i>Callipepla gambelii</i> )	11.5 (42)	7.4	162	4	10,29
California Quail ( <i>Callipepla californica</i> )	13.7 (103)	6.9	170	4	10,30
Clapper Rail ( <i>Rallus longirostris</i> )	9.6 (270)	7.5	271	5	10,31-34
Common Moorhen ( <i>Gallinula chloropus</i> )	8.7 (552)	10.5	334	5	3,35-37
American Coot ( <i>Fulica americana</i> )	8.6 (1416)	19.5	560	5	3,36,38-45
Sandhill Crane ( <i>Grus canadensis</i> )	1.9 (249)	18.3	4103 <sup>g</sup>	5	3,46-50
Common Snipe ( <i>Gallinago gallinago</i> )	3.8 (119)	9.3	116	5	3,51
American Woodcock ( <i>Scolopax minor</i> )	3.9 (266)	9.3	219	5	3,10,52
Band-tailed Pigeon ( <i>Columba fasciata</i> )	1.0 (31) <sup>h</sup>	15.5	386	4	47,53,54
White-winged Dove ( <i>Zenaida asiatica</i> )	2.0 <sup>h</sup>	21.8	153	4	47
Mourning Dove ( <i>Zenaida macroura</i> )	2.0 (703) <sup>h</sup>	19.3	115	4	3,47,55,56

<sup>a</sup>Weighted mean from listed references after adjustment for repeated data of review publications where possible. Sample size in parentheses.

<sup>b</sup>Longevity from banding records (Clapp et al. 1982; Clapp et al. 1983).

<sup>c</sup>All body mass data were extracted from Dunning (1984). Some "female" masses are for both sexes combined where sexual dimorphism does not exist or study did not differentiate.

<sup>d</sup>Ecological category determined by feeding habits outlined in Martin et al. (1951): 4, upland game birds; 5, shore birds.

<sup>e</sup>References: 1, Ellison 1974; 2, Tufts 1961; 3, Peck and James 1983; 4, Zwickel and Bendell 1967; 5, Zwickel 1975; 6, Boag 1966; 7, Bendell and Elliot 1967; 8, Kupa 1966; 9, Bump et al. 1947; 10, Schemnitz 1980; 11, Hamerstrom 1939; 12, Hart et al. 1950; 13, Sisson 1976; 14, Dalke et al. 1946; 15, McDowell 1956; 16, Porter et al. 1983; 17, Little and Varland 1981; 18, Dimmick 1974; 19, Klimstra and Scott 1957; 20, Parmalee 1955; 21, Errington 1933; 22, Klimstra 1950; 23, Klimstra and Roseberry 1975; 24, Lehmann 1946; 25, Stoddard 1936; 26, Simpson 1973; 27, Schemnitz 1961; 28, Wallmo 1956; 29, Gorsuch 1934; 30, Williams 1967; 31, Adams and Quay 1958; 32, Koziyck and Schmidt 1949; 33, Zucca 1954; 34, Stewart and Meanley 1960; 35, Causey et al. 1968; 36, Cottam and Glazener 1959; 37, Fredrickson 1971; 38, Fredrickson 1970; 39, Fredrickson 1969; 40, Provost 1947; 41, Kiel 1955; 42, Hunt and Naylor 1955; 43, Anderson 1957; 44, Miller and Collins 1954; 45, Crawford 1980; 46, Valentine and Noble 1970; 47, Sanderson 1977; 48, Walkinshaw 1949; 49, Thompson 1970; 50, Littlefield and Ryder 1968; 51, Tuck 1972; 52, Mendall and Aldous 1943; 53, Glover 1953; 54, MacGregor and Smith 1955; 55, Nice 1923; 56, Cowan 1952.

<sup>f</sup>Longevity from a life table (Campbell et al. 1973).

<sup>g</sup>Weighted mean among subspecies from Dunning (1984).

<sup>h</sup>Species-specific clutch sizes with little variance exist for these and closely related species (see Sanderson 1977; Wiley and Wiley 1979).

of all species in the sample (see Clutton-Brock and Harvey 1984; Harvey and Clutton-Brock 1985). Species were separated into taxonomical and ecological categories and relationships among traits were reexamined to eliminate this possible bias. I examined these categories to determine the effects of feeding habits (after Martin et al. 1951) and taxonomic classification on the relationships among clutch size, longevity, and body mass. Geese ( $n = 8$ ), puddle ducks ( $n = 11$ ), diving ducks ( $n = 17$ ), upland game birds ( $n = 12$ ), and shore birds ( $n = 6$ ) formed five ecological categories. Taxonomic categories were ordinal ( $n = 5$ ), familial ( $n = 6$ ), subfamilial ( $n = 9$ ), tribal ( $n = 15$ ), generic ( $n = 29$ ), and specific ( $n = 54$ ). Taxonomic classification of all species followed the American Ornithologists' Union check-list (1983).

Distributions for clutch size, longevity, and body mass data were examined for normality with Kolmogorov-Smirnov one-sample tests within each ecological or taxonomical category where sample sizes permitted (Hull and Nie 1981: p. 224), and for heterogeneity of variance with Bartlett's (1937)  $F$ -tests among categories (Nie et al. 1975: p. 422). A mean value of each life-history trait was calculated for each ecological or taxonomical category by combining data of each species assigned to each category. Differences among means of categories for each variable were examined with parametric ANOVA if data were normally distributed and variances were homogeneous ( $P > 0.05$ ), whereas means were examined with nonparametric Kruskal-Wallis ANOVA if data were not normally distributed or variances were hetero-

geneous. These tests allowed me to determine if mean life-history differences existed among ecological or taxonomical categories. Such differences could indicate that food habits and (or) taxonomy play a role in life-history evolution. The statistical relationships among category means of the three life-history traits were examined with simple, logistic (natural log), and (or) partial correlation analyses (Nie et al. 1975).

### Results

Data were obtained for 36 waterfowl and 18 shore and upland game birds (Tables 1 and 2). Clutch size and longevity were normally distributed among species whereas body mass required log transformation (natural log) to be normally distributed (all  $P > 0.05$ , Kolmogorov-Smirnov one-sample tests).

Body mass variances ( $F = 1.05$ ; 1,53 df;  $P > 0.50$ ) and means ( $\bar{x} = 984$  vs. 966 g;  $t = 0.68$ , 53 df,  $P = 0.50$ ) did not differ between Dunning's (1984) and Brough's (1983) studies among all 54 species. These results suggest that geographical or seasonal variation, effects of age, physical condition, and phenology probably do not significantly bias collective body mass means among these species. They also suggest that the body mass estimates used here are probably good estimates of each species' real mean mass.

Longevity variances ( $F = 1.24$ ; 1,25 df;  $P > 0.50$ ) did not differ between the studies of Kennard (1975) and Clapp and co-workers (Clapp et al. 1982; Clapp et al. 1983) among the 26 game bird species common to both studies. These results indicate that variances of longevity have stabilized. However, overall means ( $\bar{x} = 16.9$  vs. 11.9 years,  $t = 4.5$ , 25 df,  $P < 0.001$ ) indicated that longevity among the same 26 species increased between 1974 and 1982 (contrast Kennard 1975 with Clapp et al. 1982; Clapp et al. 1983). Kennard (1975) stated that he had poor longevity estimates for most game birds (corrected by Clapp et al. 1982; Clapp et al. 1983); therefore Kennard's (1975) longevity estimates for game birds would be expected to be lower in 1974 than those of Clapp and co-workers (Clapp et al. 1982; Clapp et al. 1983) solely from sampling error. Overall, only 28% of the longevity estimates for the 26 species treated by Kennard (1975) and Clapp and co-workers (Clapp et al. 1982; Clapp et al. 1983) increased from 1974 to 1982 and 40% of these increases were for game birds used in the present study. Additionally, the correlation between clutch size and longevity remained significant ( $P < 0.05$ ) and unchanged ( $z = 0.42$ , 93 df,  $P > 0.50$ ; Zar 1984: p. 313) when the effects of sample size of band recoveries used for longevity estimates were held constant by partial correlation analysis. These results suggest that the longevity estimates reported by Clapp and co-workers (Clapp et al. 1982; Clapp et al. 1983) and used in the present study are relatively stabilized, that small increases in the current maximum longevity will be expected over time as sample sizes of band recoveries increase, and that these longevity increases will probably not influence the relationship between clutch size and longevity for these birds (see below).

The clutch size estimates used here should be representative of each species and should not be only local estimates because data were usually collected throughout each species range, usually from hundreds of nests, and were usually collected over many years and (or) studies. Collecting clutch size data in this way probably randomized the sample of clutches for each species. Therefore, I expect the mean clutch sizes used here to be as accurate as the mean body mass estimates because potential biases towards larger or smaller clutch sizes caused by physical condition of birds, geographic location, season, or other factors are probably averaged over the studies I consulted.

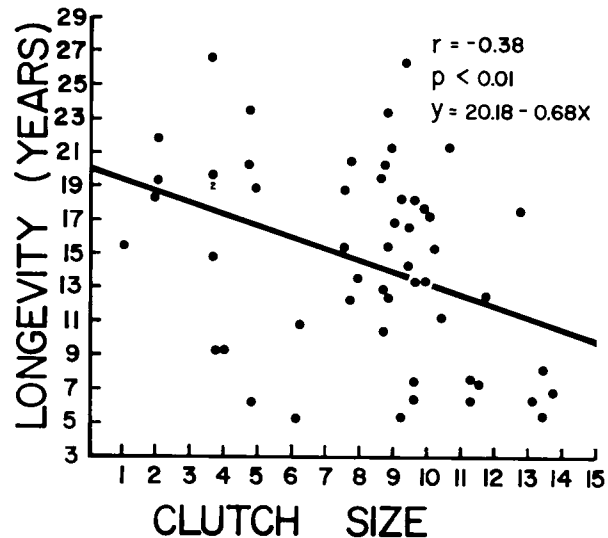


FIG. 1. The relationship between clutch size and longevity among 54 North American game birds.

Longevity was inversely correlated with clutch size ( $r = -0.38$ ,  $n = 54$ ,  $P < 0.01$ , Fig. 1) and positively correlated with logarithmic body mass ( $r = 0.38$ ,  $n = 54$ ,  $P < 0.01$ ), whereas clutch size was not correlated with logarithmic body mass ( $r = -0.18$ ,  $n = 54$ ,  $P = 0.18$ ) among all species. One could argue that longevity and clutch size were only secondarily correlated because of the primary relationship between longevity and body mass. However, longevity remained inversely correlated with clutch size when the effects of body mass were controlled with partial correlation analysis ( $r = -0.34$ , 51 df,  $P < 0.05$ ). These analyses indicate that the inverse relationship ( $P < 0.05$ ) between clutch size and longevity among these birds is not simply a function of body mass. This finding is inconsistent with results of previous studies, perhaps because previous researchers did not remove body mass effects from their life-history investigations (see Peters 1983; Calder 1984; Schmidt-Nielsen 1984).

Clutch size, longevity, and logarithmic body mass were normally distributed within all ecological and taxonomical categories (all  $P > 0.05$ , Kolmogorov-Smirnov one-sample tests) allowing parametric correlation analysis among means. However, heterogeneity of variance existed among most ecological and taxonomical categories for raw and log-transformed life-history data; nonparametric statistics were therefore required for detecting differences among means (Zar 1984). Differences among means of each life-history trait occurred among most ecological and taxonomical categories (Table 3). These results indicate that differences exist for clutch size, longevity, and body mass among species with respect to taxonomy and (or) feeding habits allowing one to test for life-history patterns among the categories.

Various degrees of relationships were found when means of ecological or taxonomical categories were examined with correlation analysis (Table 4). Clutch size remained inversely correlated with longevity ( $r = -0.50$ ,  $n = 29$ ,  $P < 0.01$ ), longevity remained positively correlated with body mass ( $r = 0.44$ ,  $n = 29$ ,  $P < 0.05$ ), and clutch size remained uncorrelated with body mass ( $r = -0.11$ ,  $n = 29$ ,  $P = 0.57$ ) when life-history values for each species were collapsed into mean values for each genus. The inverse relationship between clutch size and longevity remained for genera when the effects of body mass

TABLE 3. Statistics depicting differences among means of each life-history trait among ecological and taxonomical categories

Category	Trait		
	Clutch size	Longevity	Body mass <sup>a</sup>
Order	$H^b = 18.4; P < 0.001$	$F^b = 7.5; P < 0.001$	$F = 6.5; P < 0.001$
Family	$H = 20.4; P < 0.001$	$F = 6.2; P < 0.001$	$F = 8.0; P < 0.001$
Subfamily	$H = 27.7; P < 0.001$	$H = 20.8; P < 0.01$	$F = 18.9; P < 0.001$
Tribe	$H = 37.9; P < 0.001$	$H = 33.1; P < 0.001$	$F = 14.0; P < 0.001$
Genus	$F = 20.6; P < 0.001$	$H = 39.6; P = 0.07$	$F = 8.9; P < 0.001$
Ecology	$H = 7.8; P = 0.10$	$F = 4.3; P < 0.01$	$H = 18.8; P < 0.001$

<sup>a</sup>Species values transformed to natural logarithms before analyses.

<sup>b</sup> $H$  indicates that heterogeneity of variance existed among categories so the statistic is from Kruskal-Wallis ANOVA;  $F$  is the statistic from parametric ANOVA for samples in which heterogeneity of variance did not exist.

TABLE 4. Correlations among clutch size, longevity, and logarithmic body mass for mean values of traits for ecological and taxonomical categories

Category (sample size)	Correlations among traits		
	Clutch size vs. longevity	Clutch size vs. body mass <sup>a</sup>	Longevity vs. body mass <sup>a</sup>
Order ( $n = 5$ )	$-0.51(-0.91)^b$	$0.73(0.94)$	$0.14(0.88)$
Family ( $n = 6$ )	$-0.63(-0.66)$	$-0.09(0.27)$	$0.44(0.49)$
Subfamily ( $n = 9$ )	$-0.63(-0.69)$	$0.02(0.38)$	$0.41(0.53)$
Tribe ( $n = 15$ )	$-0.33(-0.40)$	$0.08(0.24)$	$0.41(0.46)$
Genus ( $n = 29$ )	$-0.50^{**}(-0.51)^{**}$	$-0.11(0.14)$	$0.44^{*}(0.45)^{*}$
Ecology ( $n = 5$ )	$0.23(0.59)$	$-0.31(-0.61)$	$0.65(0.78)$

<sup>a</sup>Species values transformed to natural logarithms before analyses.

<sup>b</sup>Partial correlations holding the effects of the third trait constant are given in parentheses.

\* $P < 0.05$ .

\*\* $P < 0.01$ .

were controlled ( $r = -0.51$ , 26 df,  $P < 0.01$ ). However, no other significant (all  $P > 0.05$ ) simple or partial correlations were found among mean values of life-history traits for higher taxonomical categories (ordinal, familial, subfamilial, tribal), nor did any significant correlations exist for mean values of traits for ecological categories, perhaps because of low sample sizes within categories (Table 4; see Discussion).

### Discussion

Species and genera with larger clutch sizes live shorter lives than those with smaller clutch sizes, and body mass has an insignificant influence on this relationship. Thus, the evolution of longevity may be influenced by clutch size or the evolution of clutch size may be influenced by longevity among these species. There is support for the hypotheses that the costs of reproduction are manifested as a reduction in survival and that mortality is balanced by clutch size among these birds. Thus, life histories among game birds may have evolved in a fashion consistent with the fecundity-survival trade-off and balanced mortality hypotheses.

It may be useful to consider why this pattern has emerged. First, birds with larger clutch sizes may use so much more energy than those with smaller clutch sizes that they forfeit energy needed to survive. Second, longer-lived individuals with smaller clutch sizes may achieve similar reproductive success during their lifetimes as shorter-lived individuals achieve with larger clutch sizes. Third, large clutch size and long life should

eventually lead to perpetual population increase, unsupportable by any environment, whereas small clutch size and short life should eventually cause extreme rarity. Perhaps few species exist with either of these life-history patterns because both of them easily lead to extinction (J. S. Millar, personal communication). I conclude that the evolution of clutch size is influenced by longevity or that the evolution of longevity is influenced by clutch size, and that we cannot determine the cause or effect trait at this time (see also Ekman and Askenmo 1986: p. 166).

The small influence of body mass on the relationship between clutch size and longevity was not expected in light of previous studies which indicated strong influences of body mass on avian survival and reproduction (see Western and Ssemakula 1982; Peters 1983; Calder 1984). However, none of these studies attempted to remove the effects of body mass from their life-history investigations, effects that could have biased their conclusions. Alternatively, perhaps the dependency of life-history variables on body mass varies between the mostly precocial (51 of the 54 species) game and most altricial nongame birds. Unfortunately, previous studies relating body mass to life-history traits seldom indicate which species were studied to test this hypothesis (see Peters 1983). The inverse relationship between clutch size and longevity reported here may not hold for nongame species since they usually expend proportionately less energy with respect to basal metabolic rate (191% vs. 45%) for clutch production and therefore may have lower reproductive costs and a different dependency on body

mass than waterfowl, shore, or gallinaceous birds (Ricklefs 1974: p. 191). This consideration could also explain the discrepancy between the present and previous studies.

The inverse relationship between clutch size and longevity and the positive relationship between longevity and body mass disappear ( $P > 0.05$ ) for mean life-history traits among higher taxonomic levels and among ecological categories even though differences exist among mean life-history traits (Tables 3 and 4). This finding indicates that although food habits and taxonomy seem to influence mean life-history traits among these birds (Table 3), the influence does not produce definable patterns. However, these results may simply be due to the low sample sizes among higher taxonomic levels and ecological categories or to the relatively small amount of variance in common among the three life-history variables (range of  $r^2 = 3.2\text{--}14.3\%$ ). Further study with more species may be necessary to determine whether patterns among clutch size, longevity, and body mass are prevalent at taxonomic levels above genus and for ecological categories. Results presented here indicate that no patterns exist ( $P > 0.05$ ) even though some correlation coefficients are very large and most signs of those coefficients are in the same direction as signs among species and genera (see Table 4). For example, large partial correlation coefficients are found at the ordinal level but they are insignificant ( $P > 0.05$ ) with a sample size of only five orders and 2 degrees of freedom.

Almost all intraspecific studies on birds have examined the fecundity–survival trade-off hypothesis in hole nesters (Kluyver 1963, 1971; Askenmo 1979; Bryant 1979; De Steven 1980; Hogstedt 1981; Ekman and Askenmo 1986). The only previous study on natural populations of open nesters found a positive relationship between clutch size and survival in song sparrows, *Melospiza melodia* (Smith 1981). While most species in the present study were open-nesters, the data do not confirm Smith's (1981) observation. However, patterns between reproduction and survival within species may be different from patterns among species. A few individuals within a population may be able to exhibit phenotypic plasticity of increased clutch size, longevity, and body mass simultaneously, whereas consistent increases for these traits for all individuals of a species require major changes in design and (or) unlimited resources. Consistent selection for larger clutch size and greater survival is probably impossible for any population to maintain without environmental deterioration because more and more individuals are born while more and more survive longer, causing overpopulation. However, some individuals of a population could maintain both variables at high values at the expense of other individuals (i.e., through territoriality, dominance, locally abundant resources, etc.; see Fretwell 1969), and thus a positive relationship between clutch size and survival becomes possible within a population.

Although the fecundity–survival hypothesis is studied for many more species in the present study than in all previous studies combined, results presented here must be viewed in context. The relationship between reproduction and survival among species may be radically different from the relationship within species (Bell 1984b). Where clutch size increases with age, large clutch size and increased survival could occur as a by-product of an older age structure within a population (Coulson and White 1958; Pugesek 1980, 1983; Pugesek and Diem 1983), whereas clutch size and survival may be inversely correlated among species. Indeed, it has been argued that interspecific studies should not be used to study some aspects of the fecundity–survival trade-off hypothesis (see Bell 1980,

1984a). However, these aspects deal with the direct costs of reproduction to specific individuals which the present interspecific study cannot examine. The intent here was to study the overall relationship between clutch size and longevity among bird species. This relationship was found to be inverse when many species or genera are considered, uninfluenced by body mass, and therefore perhaps important in the evolution of avian life histories (see De Steven (1980) for an alternative view).

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