Reproductive strategies in waterfowl: the effect of ultimate environmental factors, size and phylogeny

Terhi Laurila

Laurila, T. 1988: Reproductive strategies in waterfowl: the effect of ultimate environmental factors, size and phylogeny. — Ornis Fennica 65:49–64.

Using data extracted from the literature, I studied the world's waterfowl species (142 species from the total of 149) in order to reveal the ultimate factors contributing to the evolution of their reproductive strategies. As the differences between species reflect not only optimal adaptations to the environment, but also phylogenetic relationships or differences in size, special care was given to separate the effects of ecological factors from those due to size and phylogeny.

Body weight scaled allometrically to all traits studied. Increased body size was accompanied by decreasing clutch size and an increasing trend in all other dependent variables. When reproductive traits were adjusted for the effect of weight, a rapid rate of development in the young accompanied northern distribution and ground-nesting habits. Large eggs were combined with young that were at an advanced stage at hatching. In general, late age at maturity and decreasing nest concealment were associated with small clutches, but the reasons for evolving a small clutch did not seem to be the same in different species.

Using principal component analysis, the factors influencing reproductive traits were grouped into three main components, interpreted as size, geography and tribe. Together these explained 80–95% of the variation in other traits, but only 55% of the clutch size variation. Thus given the size, distribution and phylogeny of a waterfowl species, its reproductive strategy is determined to a great extent. A way to change reproductive strategy, therefore, is to change body size. Further adaptation can be achieved by modifying clutch size, as it is the trait least determined by the three main factors.

Terhi Laurila, Dept. of Zoology, Univ. of Helsinki, P. Rautatiekatu 13, SF-00100 Helsinki, Finland.

Introduction

The waterfowl species of the world have very different reproductive strategies. The mean clutch size varies from 2 to 14 eggs, and the relation of clutch mass to female weight from 16 up to 100% (Lack 1967, Johnsgard 1973). What are the ultimate ecological factors behind the evolution of such different strategies?

Most theories of the ultimate factors in waterfowl have concentrated on clutch size determination. Lack (1967, 1968) proposed that the waterfowl clutch size is limited by the food resources available to the female around the time of laying, and that these limited resources could be used to form either a few large eggs or a greater number of smaller ones. He suggested that large eggs were advantageous in certain conditions because they either allowed the newly hatched duckling to have a greater fat reserve or to hatch at a more advanced stage. Klomp (1970) supported this view, while Johnsgard (1973) did not believe that the food hypothesis applied to other waterfowl than geese nesting in the arctic. He suggested that the waterfowl clutch size is generally limited by the amount of young the parents can care for, a decreased available optimum breeding period and an increased probability of nest predation.

Winkler & Walters (1983) reviewed the problem of clutch size determination in precocial birds, relating reproductive effort to the birds' life history. They took into account the fact that long-lived birds can afford to have smaller clutches (Charnov & Krebs 1974, Goodman 1974), as individuals try to maximize their reproductive effort over their lifetimes rather than within a single breeding attempt (Williams 1966, Schaffer 1974).

None of these theories, however, considered the possibility that the reproductive traits of waterfowl species with different ecology reflect the body size or phylogenetic relationships rather than ecological factors. In other groups of birds, as well as in mammals, reproductive traits have been shown to scale allometrically with body size (Rahn et al. 1975, Blueweiss et al. 1978, Western & Ssemakula 1982, Stearns 1983, Saether 1985 and 1987) so that larger species tend to have smaller clutches than smaller species.

Also, all traits do not reflect optimal adaptations to the environment but rather common ancestors (Wanntorp 1983, Elgar & Harvey 1987). A species can evolve only within the constraint set by the taxonomic unit in which it belongs (e.g. Tuomi et al. 1983). For example, if all northern species belong to related taxonomic units, their small clutches could be due to the phylogenetic relationship and not to the geographic distribution.

The aim of my study was to investigate the possible ultimate factors contributing to the evolution of the different reproductive strategies in waterfowl, taking into account the effect of body size and phylogeny. As the previous theories in waterfowl focused on clutch size, I wanted to examine if the reasons for evolving a small clutch could be the same for different species.

Material and methods

Data were gathered from various handbooks (Delacour 1954–1959, Johnsgard 1965, 1978, Bauer & Glutz von Blotzheim 1968–1969, Kolbe 1972, Palmer 1976, Cramp 1977, Fjeldså 1977, Brown et al. 1982, Frith 1983, Bezzel 1985). The systematic order follows Johnsgard (1978). When a species had subspecies, I used the information on the nominate race only. I preferred most recent information as a rule, but when information in recent handbooks differed considerably, the mean of the reported values was taken. The great variation in the reported values is due to the fact that, for example, age at fledging is difficult to determine in ducks (Lack 1968), and the values of different populations, or captive versus wild birds, vary considerably. If the habits of the species were not known or nothing special was reported about them, I usually assumed that they followed the pattern of the genus or tribe. This may have caused some mistakes. Errors also arise because some species are well studied, whereas the information on others may stem from a single reference. However, to put it in Lack's words (1968), "many of the trends brought out are so striking that they would not be appreciably affected by minor changes of this sort". Only very scanty information was available for seven species, so I excluded them from the analyses (Table 2). Data were thus obtained for 142 out of the total of 149 waterfowl species. The data are available from the author upon request.

Dependent variables

The average female weight (g), mean wing length for both sexes (mm), clutch size, egg weight (g), clutch mass (egg weight x clutch size (g)), incubation period (d), age at fledging (d) and the time required for breeding (clutch size + incubation period + age at fledging (d)) were considered to reflect the size and reproductive effort of the species and were used as dependent variables in the analyses.

Female weight was preferred to the mean weight of the sexes because some species had a marked size dimorphism and only females lay eggs. For the few species for which the incubation period was unknown, it was estimated by simple linear regression from wing length. The extremely long incubation period of 43 days for the Torrent Duck (*Merganetta armata*), reported by Moffet (1970), would have been a statistical outlier and was therefore not used in the statistical analyses but replaced by the values predicted by the regression from wing length (25 days).

Independent variables

Other information of the species was used as independent variables. I coded these as follows:

Breeding range (the range, in latitudes, where breeding occurs regularly; introduced populations were not taken into account).

1. Restricted (2–20)
2. Intermediate (21–40)
3. Wide (41–115)

Distance from the equator (the northernmost, or southernmost — for southern hemisphere species, limit of the breeding range, in latitudes).

1. Tropical (0–30)
2. Temperate (31–60)
3. Arctic (61–90)

Mating system

1. Monogamous, permanent pair-bond
2. Monogamous, seasonal pair-bond
3. Polygamous

Feeding type

1. Feeding mainly by grazing
2. Feeding mainly by dabbling
3. Feeding mainly by diving
4. Feeding mainly by diving and grazing

For the ANOVAs these were recoded as follows:

1. Feeding mainly by diving (code 3)
2. Feeding mainly by dabbling or grazing (codes 1, 2)

Age at maturity

1. Mature in the first year of life
2. Mature in the second year of life
3. Mature in the third or in a later year of life

Nest concealment

1. Nest on the ground, usually not concealed from above
2. Nest on the ground, usually concealed from above
3. Nest in a hole or cavity

Paternal care

1. No male guarding
2. Male leaves female after laying
3. Male stays for some time after laying
4. Male helps in brooding
5. Male defends a territory and helps in brooding
6. Male defends a territory, incubates and helps in brooding

For the ANOVAs these were recorded as follows:

1. Male helps in brooding (codes 4–6)
2. Male leaves female before hatching of the young (codes 1–3)

Independence of the young

1. Young independent after fledging
2. Young independent at fledging
3. Young independent before fledging
4. Yound independent soon after hatching

As the whole material comprised only one family I used species as the taxonomic unit for comparisons.

Statistical methods

Statistical models require that the sampling of individuals is done at random. Taxonomic data cause some difficulties in statistical analyses as they are not sampled randomly. Species belonging to the same taxonomic unit resemble each other more than species belonging to different units. Nonrandomness of sample selection may be reflected in lack of independence of the items, nonnormal distribution or a correlation between the means and the variances, which in their turn affect the validity of the tests (Sokal & Rohlf 1981). In order to minimize these difficulties, dependent variables were transformed with logarithms prior to the statistical analyses.

Dependent variables were adjusted for the effect of female weight as follows: simple linear regression for weight and each dependent variable was computed and the weight for the species multiplied by the appropriate regression coefficient (Table 3). This sum was subtracted from the actual value of each dependent variable for the species in question (see Stearns 1983).

Correlation coefficients were computed using product-moment correlations (r) for dependent (continuous) variables and Spearman rank-correlations (rs) for independent (ranked) variables or when one ranked variable was correlated with weight. In order to find out if the correlation of any two independent variables depended on causes other than correlation with weight, partial correlations (r_p) were computed from the rank correlations (Sokal & Rohlf 1981).

The effect of independent variables on weight and reproductive traits, and the differences between tribes, were studied with one-way analysis of variance. The effect of independent variables was studied

Table 1. Means, standard deviations (SD), ranges and coefficients of variation (CV) for traits reflecting size and reproductive output in Anatidae (n = number of species. All variables untransformed).

Trait	n	Mean	SD	Range	CV between tribes	Mean CV within tribes
Female weight, g	142	1449	1614	200–10500	111	48
Egg weight, g	142	81	61	23–340	75	33
Clutch mass, g	141	568	316	174–2040	56	39
Wing length, mm	142	273	104	130–617	38	16
Age at fledging, d	104	61	18	35–160	30	21
Clutch size	141	8	2	2–14	28	22
Time required for breeding, d	104	96	21	66–207	22	14
Incubation period, d	142	28	3	22–43	12	8

Table 2. Means and standard deviations (SD) for the studied traits, and variation in the independent variables in the nine tribes of Anatidae, consisting of more than one species (n = number of species. All variables untransformed). Mating system: MP = monogamous, permanent pair-bond, MS = monogamous, seasonal pair-bond, P = polygamous. Feeding type: DG = dabbling or grazing, DIV = diving. Paternal care: P = present, A = absent. Nest concealment: NC = not concealed from above, C = concealed from above, H = in holes or cavities. Independence of young: AF = after fledging, F = at fledging, BF = before fledging, AH = after hatching.

Trait		Anserini swans and true geese	Tachyerini steamer ducks	Tadornini sheldgeese and -ducks	Cairinini perching ducks	Mergini sea ducks	Aythyini pochards	Dendrocygnini whistling ducks	Oxyurini stiff-tailed ducks	Anatini dabbling ducks	P
Female	n	22	3	14[§]	13	16[§]	16	9	8	37[§]	
weight, g	mean	3870	3367	1724	1159	986	824	764	694	620	***
	SD	2571	850	713	1295	458	219	184	326	239	
Wing length,	mean	447	278	354	262	231	215	214	161	221	***
mm	SD	78	15	43	105	35	24	28	21	35	
Clutch size	mean	5	7	8	10	8	9	10	5	8	***
	SD	1	0	2	2	2	1	2	2	2	
Egg weight,	mean	181	143	93	53	67	56	49	85	45	***
g	SD	87	26	23	32	19	9	15	24	14	
Clutch mass,	mean	934	1001	755	506	514	498	483	442	358	***
g	SD	481	184	175	312	167	112	117	160	100	
Incubation	mean	30	31	30	29	28	26	29	25	26	***
period, d	SD	5	0	1	3	3	1	2	1	2	
Age at fledging, d	mean	66	84	70	67	57	58	59	56	53	ns
	SD	34	0	14	9	10	8	15	3	10	
Time required	mean	100	122	109	107	93	93	98	87	88	ns
for breeding, d	SD	39	0	13	9	12	9	16	3	11	
Age at maturity, yr	mean	3	2	2	1	2	2	1	1	1	–
	SD	0.5	0	0.2	0.2	0.4	0.5	0	0.4	0.2	
Distance from	mean	67	54	42	34	74	54	29	45	52	–
the equator, latitudes	SD	14	2	15	11	7	15	9	10	15	
Breeding range,	mean	20	11	24	39	27	24	41	42	39	–
latitudes	SD	9	8	15	16	10	11	20	34	23	
Mating system		MP	MP	MP	MP,MS (P)	MS	MS	MP	MS (P)	MP,MS	–
Feeding type		DG	DIV	DG	DG	DIV	DIV	DIV,DG	DIV	DG(DIV)	
Paternal care		P	P	P	P,A	A	A	P	A	P,A	
Nest concealment		NC	C	H (NC,C)	H (C)	H (NC,C)	C	C	C	C (NC,H)	
Independence of young		AF	?	AF (F)	AF (F)	BF	BF	AF	AH	F (BF)	

[§] *Tadorna cristata, Camptorhynchus labradorius, Mergus squamatus, Mergus octosetaceus, Mergus australis, Anas bernieri, Anas melleri* are not included, due to scanty information

Levels of significance *(P≤0.05), **(P≤0.01), ***(P≤0.001), ns = nonsignificant both prior to and after adjusting the traits for the effect of weight. Differences between the means were tested with F-tests.

Principal component analysis was used in order to reveal the main factors behind the variation in the dependent variables. Analysis was performed of correlation matrix. Unrotated factor loadings were used to estimate the percent of variation in each trait, explained by the principal components.

Results

Variability of the traits

"Average waterfowl" weighted about 1.5 kg, matured in its second year, laid eight eggs weighing about 80 grams each, incubated them for 28 days, and the young fledged after 60 days. The average time required for breeding was about three months. There was, however, considerable variation in most traits (Table 1).

If the whole family Anatidae is studied, the traits reflecting size varied most (had largest CVs), whereas those reflecting the rate of development and clutch size varied less (Table 1). This trend was also the same within the tribes, although the amount of variation in all traits, except clutch size, was approximately halved. Clutch size varied almost as much within the tribes as between them (Table 1).

However, the amount of variation was not uniform within the different tribes. Some tribes consist of species of largely varying size and reproductive effort, whereas the species of others vary remarkably little (Table 2). Tribes were even more conservative with respect to ecological factors. Rate of independence in the young varied only negligibly within the tribes, and the type of feeding and degree of paternal care varied very little. The mating system and degree of nest concealment varied in some tribes but not in others (Table 2).

The effect of body size

Female weight scaled allometrically with all reproductive traits. Increased body size was accompanied by decreasing clutch size, and an increasing trend in all other dependent variables. Wing length and egg weight were the traits most connected with female weight, while clutch size and the time required for breeding varied more independently (Table 3).

Table 3. Regressions (b) and 95% confidence limits (CL) for the regression coefficient of each dependent variable with female weight in Anatidae (R^2 = coefficient of determination).

Trait	b	CL	P	R^2
Egg weight	0.661	±0.025	***	83
Wing length	0.393	±0.016	***	82
Clutch mass	0.518	±0.026	***	74
Incubation period	0.074	±0.012	***	25
Age at fledging	0.104	±0.022	***	14
Time required for breeding	0.074	±0.016	***	13
Clutch size	–0.143	±0.031	***	13

Levels of significance * ($P\leq0.05$), ** ($P\leq0.01$), *** ($P\leq0.001$)

Female weight correlated significantly ($P\leq0.05$ in all cases) with the independent variables as well. Large waterfowl species tended to have restricted ($r_s=-0.30$), northern ($r_s=0.21$) breeding ranges, late age at maturity ($r_s=0.70$), grazing habits ($r_s=-0.34$), permanent pair-bonds ($r_s=-0.35$), poorly-concealed nests ($r_s=-0.48$), extended paternal care ($r_s=0.24$) and young that spend a long time with their parents ($r_s=-0.61$).

Correlations between the variables

All dependent variables covaried with body size. Indeed, most correlations between the reproductive traits were due to this covariation; when dependent variables were adjusted for the effect of female weight, only a few significant ($P\leq0.05$ in all cases) correlations remained. Irrespective of body size, species with small clutches tended to have large eggs ($r=-0.58$), species with long incubation periods also had long fledging periods ($r=0.53$), and species with large clutch masses had a slow rate of development (clutch mass vs. incubation period, $r=0.35$, vs. age at fledging, $r=0.34$) and vice versa.

Independent variables were also intercorrelated. Most of these correlations also arise from the covariation of both traits with weight. When the effect of weight was taken into account the following significant ($P\leq0.01$ in all cases) correlations remained: species with wide breeding ranges tended to mature early ($r_p=-0.28$); late age at maturity, decreasing nest concealment and little paternal care were associated with northern breeding ranges (distance from the equator vs. age at maturity, $r_p=0.40$, vs. nest concealment, $r_p=-0.33$, vs. paternal care, $r_p=-0.23$); permanent pair-bonds were associated with increas-

Table 4. Means and limits for mean ± standard deviation (L) for the dependent variables in tropical, temperate and arctic waterfowl species, prior to accounting for the effect of body weight (n = number of species. Analyses performed on logarithmically transformed variables).

Trait		Northernmost range of breeding			Significance prior/after acc. for weight	
		tropical	temperate	arctic		
Female weight, g	n	18	76	48		
	mean	994	866	1269	*	–
	L	550–1797	397–1891	541–2975		
Wing length, mm	n	18	76	48		
	mean	263	238	285	*	ns
	L	200–347	170–335	200–408		
Clutch size	n	18	75	48		
	mean	8.4	7.6	6.9	ns	ns
	L	6.0–11.6	5.6–10.3	5.1–9.4		
Egg weight, g	n	18	76	48		
	mean	59	64	77	ns	*
	L	39–89	37–111	40–147		
Clutch mass, g	n	18	75	48		
	mean	493	485	534	ns	ns
	L	317–765	294–802	332–859		
Incubation period, d	n	18	76	48		
	mean	29	28	27	**	***
	L	27–32	25–31	24–30		
Age at fledging, d	n	10	48	46		
	mean	67	63	52	***	***
	L	55–83	50–79	40–67		
Time required for breeding, d	n	10	48	46		
	mean	106	100	86	***	***
	L	92–121	85–119	71–105		

Levels of significance * (P≤0.05), ** (P≤0.01), *** (P≤0.001), ns = nonsignificant.

ing paternal care (r_p=–0.81) and late independence of young (r_p=0.78); diving species tended to have more independent young than grazing or dabbling species (r_p=0.74).

The effect of independent factors on reproductive traits

Distance from the equator. Waterfowl species breeding in the arctic were significantly heavier than tropical or temperate species (Table 4). When the effect of weight was accounted for, arctic species had significantly shorter incubation and fledging periods, and required less time for breeding than more southern species (Table 4). Tropical species had significantly smaller eggs for their size, than temperate or arctic species. Arctic species did not have significantly smaller clutches than other species, in relation to their size, so it seems that the small clutches of many arctic waterfowl species can be attributed to other causes, rather than solely to the breeding latitude (Table 4).

Age at maturity. Late-maturing species were significantly heavier than species maturing earlier (Table 5). After adjusting the traits for the effect of weight, late-maturing species had significantly smaller clutches and clutch masses, as well as shorter incubation and fledging periods, and total required breeding time, than earlier maturing species (Table 5). As late age at maturity accompanied northern breeding ranges (Table 6), the faster rate of development in the young of late-maturing species is probably due to their northern breeding ranges and not to the age at maturity.

Nest concealment. Species with nests that were not concealed from above were significantly heavier than either hole-nesters or species with well-concealed nests (Table 7). After accounting for the effect of weight, they also had significantly smaller

Table 5. Means and limits for mean ± standard deviation (L) for the dependent variables in waterfowl species mature in their first, second or third (or later) year, prior to accounting for the effect of body weight (n = number of species. Analyses performed on logarithmically transformed variables).

Trait		Age at maturity 1	2	3	Significance prior/after acc. for weight	
Female weight, g	n	72	41	20		
	mean	598	1253	3044	***	–
	L	397–900	643–2441	1559–5943		
Wing length, mm	n	72	41	20		
	mean	207	274	424	***	ns
	L	171–251	205–365	330–545		
Clutch size	n	71	41	20		
	mean	8.2	7.4	5.2	***	**
	L	6.2–10.7	5.4–10.2	4.3–6.3		
Egg weight, g	n	72	41	20		
	mean	47	83	149	***	ns
	L	33–65	51–133	90–245		
Clutch mass, g	n	71	41	20		
	mean	380	612	773	***	**
	L	273–531	393–951	476–1254		
Incubation period,	n	72	41	20		
	mean	27	29	28	***	*
	L	24–29	26–32	25–33		
Age at fledging, d	n	47	33	19		
	mean	55	63	56	*	**
	L	46–66	48–84	40–80		
Time required for breeding, d	n	47	33	19		
	mean	90	101	91	*	**
	L	79–103	82–124	70–117		

Levels of significance as in Table 4.

Table 6. Number of species belonging to different ecological groups in tropical, temperate and arctic regions.

Ecological factor	Region Tropical	Temperate	Arctic
Paternal care			
present	12 (16%)	44 (60%)	17 (18%)
absent	5 (8%)	31 (46%)	31 (46%)
Nest concealment			
not concealed from above	3 (9%)	9 (27%)	21 (64%)
concealed from above	7 (11%)	36 (56%)	21 (33%)
in holes or cavities	7 (25%)	15 (54%)	6 (21%)
Age at maturity			
mature in the first year of life	9 (13%)	49 (68%)	14 (19%)
second	3 (7%)	21 (52%)	17 (41%)
third or later	1 (5%)	2 (10%)	17 (85%)
Mating system			
monogamy, permanent pair-bond	11 (18%)	34 (55%)	17 (27%)
monogamy, seasonal pair-bond	2 (3%)	38 (54%)	31 (43%)
polygamy	4 (57%)	3 (43%)	0 (0%)

Table 7. Means and limits for mean ± standard deviation (L) for the dependent variables in waterfowl species with varying degrees of nest concealment, prior to accounting for the effect of body weight (n = number of species. Analyses performed on logarithmically transformed variables).

Trait		Nest on ground not conc.	Nest on ground concealed	in holes or cavities	Significance prior acc. for weight	Significance after acc. for weight
Female weight, g	n	33	64	28		
	mean	2477	805	760	***	–
	L	1186–5177	441–1470	402–1435		
Wing length, mm	n	33	64	28		
	mean	388	223	246	***	***
	L	291–516	175–285	183–331		
Clutch size	n	33	64	28		
	mean	5.5	8.0	9.0	***	***
	L	4.5–6.8	6.2–10.2	7.0–11.6		
Egg weight, g	n	33	64	28		
	mean	127	57	56	***	ns
	L	70–230	37–88	37–84		
Clutch mass, g	n	33	64	28		
	mean	701	453	505	**	***
	L	406–1211	301–682	322–790		
Incubation period, d	n	33	64	28		
	mean	28	27	30	***	***
	L	24–33	25–30	27–33		
Age at fledging, d	n	29	45	20		
	mean	60	56	62	ns	ns
	L	41–88	46–69	54–71		
Time required for breeding, d	n	29	45	20		
	mean	94	92	102	ns	*
	L	70–127	79–106	94–111		

Levels of significance as in Table 4.

clutches, whereas the clutch size of hole-nesting species and species with well-concealed nests did not differ from each other (Table 7). Hole-nesters had significantly longer incubation periods and larger clutch masses than other species (Table 7). These trends might be due to the breeding latitude, as hole-nesters are fewer in the arctic (Table 6), but the trends were actually the same, irrespective of the latitude.

Paternal care. Species where males shared in brood rearing were significantly heavier than those where they did not (Table 8). When traits were adjusted for the effect of weight, species with paternal care had significantly smaller clutches and longer incubation periods than species where males did not care for the young (Table 8). As the latter species tended to have a northern distribution as well (Table 6), the trend in the incubation period may be due to the breeding latitude.

Independence of young. Species with late independence of young were significantly heavier than species with more independent young (Table 9). When the effect of weight was accounted for, species with very precocial young had significantly shorter wings, smaller clutches and larger eggs than other species (Table 9).

Breeding range, mating system and feeding type. The reproductive traits of species with different breeding ranges, mating systems and feeding types did not differ significantly from each other, after the effect of body size was taken into account. Therefore, the results of these analyses are not shown in separate tables.

Table 8. Means and limits for mean ± standard deviation (L) for the dependent variables in waterfowl species with varying degrees of paternal care, prior to accounting for the effect of body weight (n = number of species. Analyses performed on logarithmically transformed variables).

Trait		Paternal care Present	Paternal care Absent	Significance prior/after acc. for weight	
Female weight, g	n	73	67		
	mean	1297	766	***	–
	L	513–3281	455–1289		
Wing length, mm	n	73	67		
	mean	294	222	***	***
	L	199–434	178–277		
Clutch size	n	73	66		
	mean	6.8	8.2	***	*
	L	5.0–9.4	6.1–10.9		
Egg weight, g	n	73	67		
	mean	82	55	***	ns
	L	42–160	38–80		
Clutch mass, g	n	73	66		
	mean	562	449	**	ns
	L	321–982	314–642		
Incubation period, d	n	73	67		
	mean	29	27	***	*
	L	26–33	24–29		
Age at fledging, d	n	52	52		
	mean	62	55	*	ns
	L	45–84	46–66		
Time required for breeding, d	n	52	52		
	mean	98	91	*	ns
	L	78–124	79–104		

Levels of significance as in Table 4.

In short: As age at maturity reflects longevity (Western & Ssemakula 1982) and nest concealment the rate of predation (Perrins 1977), the factors combined with: (a) the rate of development in the waterfowl young, were distance from the equator and nest predation; (b) large eggs, were distance from the equator and precociality of the young; and (c) small clutches, were a long-life span, increased paternal care, increased nest predation and extremely precocial young.

The relative importance of factors affecting dependent variables

As both independent and dependent factors were more or less correlated, it might be more informative to group the factors affecting reproductive traits. Principal component analysis revealed three main components that together explained 55 to 95% of the variation in dependent variables (Table 11).

The first principal component had strong positive loadings on age at maturity, female weight, egg weight and wing length, and negative loadings on nest concealment and clutch size (Table 10). So the first principal component arranges the species from small, early-maturing and highly fecund to the opposite. One might therefore call the first principal component a "size" factor.

The second principal component had the strongest positive loadings on the time required for breeding, age at fledging, incubation period and clutch mass, and the strongest negative loading on the distance from the equator (Table 10). The principal component

Table 9. Means and limits for mean ± standard deviation (L) for the dependent variables in waterfowl species with varying degrees of independence in the young, prior to accounting for the effect of body weight (n = number of species. Analyses performed on logarithmically transformed variables).

		Young independent				Significance prior/after acc. for weight	
Trait		after fledging	at fledging	before fledging	after hatching		
Female weight, g	n	39	19	36	7		
	mean	2237	704	792	574	***	–
	L	1012–4944	427–1161	515–1216	444–742		
Wing length, mm	n	39	19	36	7		
	mean	379	238	222	154	***	***
	L	280–513	185–306	193–254	141–169		
Clutch size	n	39	19	36	6		
	mean	6.2	8.4	8.3	5.7	***	**
	L	4.6–8.3	5.5–12.7	6.7–10.3	4.4–7.3		
Egg weight, g	n	39	19	36	7		
	mean	116	52	56	76	***	***
	L	62–217	33–80	42–76	59–98		
Clutch mass, g	n	39	19	36	7		
	mean	713	434	465	451	***	ns
	L	437–1163	281–670	339–640	381–640		
Incubation period, d	n	39	19	36	7		
	mean	29	27	27	25	**	ns
	L	26–33	23–32	25–29	24–26		
Age at fledging, d	n	31	15	29	4		
	mean	64	52	56	55	ns	ns
	L	44–92	44–63	46–68	53–58		
Time required for breeding, d	n	31	15	29	4		
	mean	100	89	91	87	ns	ns
	L	76–132	77–102	80–105	84–91		

Levels of significance as in Table 4.

Table 10. Rotated factor loadings of the traits on the first three principal components (PCA). Loadings <|0.3| are not shown.

Trait	PCA 1	PCA 2	PCA 3
Age at maturity	0.82		
Female weight	0.78	0.45	–0.36
Nest concealment	–0.74		
Egg weight	0.74	0.50	–0.30
Wing length	0.72		–0.54
Distance from the equator	0.67	–0.38	0.44
Clutch size	–0.59		
Clutch mass	0.55	0.70	
Feeding type	–0.37		0.70
Tribe			0.90
Mating system			0.80
Incubation period		0.86	
Paternal care			–0.91
Time required for breeding		0.96	
Age at fledging		0.93	

Table 11. Percent variance in the dependent variables explained by the first three principal components (PCA) (analysis performed on logarithimically transformed variables).

Trait	Percent variance explained by PCA 1	PCA 2	PCA 3	Total
Female weight	87	3	5	95
Time required for breeding	27	57	9	93
Egg weight	83	1	8	92
Wing length	83	5	0	88
Age at fledging	29	47	11	87
Incubation period	40	36	5	81
Clutch mass	66	4	9	79
Clutch size	29	25	1	55

arranges species from those with a slow rate of development, large clutch masses and southern ranges to the opposite, and might be called the "northernness" factor.

The third principal component had the strongest positive loadings on tribe, mating system and feeding type, and negative loadings on degree of paternal care (Table 10). It thus arranges species from those with permanent pair-bonds, grazing or dabbling habits and extended paternal care to the opposite. As all these traits vary very little within the tribes but greatly between them, and because of the strong loading on tribe, one might call the third principal component a "tribe" or "phylogeny" factor.

The first principal component explained more than 80% of the variation in female weight, egg weight and wing length, and the least (about 30%) of the variation in age at fledging and clutch size (Table 11). The second principal component explained mostly the variation in traits reflecting the rate of development and clutch size, whereas the third principal component explained mostly the variation in age at fledging, time required for breeding, clutch mass and egg weight (Table 11). Together the three principal components explained 80%, or more, of the variation in all other traits but only 55% of the clutch size variation (Table 11).

Discussion

The effect of body size

In this study most of the differences in reproductive traits between different waterfowl species were due to differences in size. Increased body size has been accompanied by a large offspring weight, few offspring and a slow rate of development in other groups of birds, as well as in mammals (Stearns 1983, Saether 1987). The absolute values of the correlations between weight and reproductive traits are smaller in this study because of the smaller taxonomic unit studied.

Judging by the extent of the breeding range, it would seem that small species are more successful than large. Why then have some species evolved a weight of 4 or 10 kg? Most of the large species are northern and have poorly concealed nests, prone to predation. Their large body size may have evolved as a defence against predators. Also, the costs of temperature regulation are relatively smaller for large birds (Kendeigh 1969).

The correlations between body size and ecological factors such as age at maturity, paternal care, nest concealment and the degree of independence in the young, illustrate that body size is an integrated part of an animal's life history, as has been argued (Saether 1987) and its effect on reproductive traits cannot actually be "removed". However, one is usually not so interested in the general trend, which seems to be fairly similar in most groups of animals, as in the exceptions. In order to study whether the reproductive traits of species with a differing ecology are due to the ecological factors or to differences in size, one must somehow take the allometry into account. Therefore, the interest is focused on species with reproductive traits exceptional for their size.

The effect of phylogeny and ecological factors

Do the significant relationships I found between some ecological factors and reproductive traits in waterfowl reflect a real causal relationship, merely a covariation of these traits, or common ancestors? Elgar & Harvey (1987) suggest that trends caused by ecological factors and not merely by common ancestors should be the same between, and within, taxonomic units (tribe or genus in this study as only one family was studied). However, most ecological traits do not vary within tribes and still less within genera in this study (Table 2). Thus within-tribe comparisons are of limited value in this study. I, therefore, compared the effects or ecological factors on reproductive traits in the whole data set and in the subfamily Anatinae. (The subfamily Anserinae — consisting of only 3 tribes — was not chosen because of the great similarity in ecological factors between the tribes in this subfamily).

The effect of ecological factors was the same in the whole data set and within Anatinae, with the exception of age at maturity and paternal care. Virtually all species of Anatinae mature at, or before, their second year of life, so the effect of late age at maturity cannot be studied in this group. The degree of paternal care did not have any effect on clutch size in Anatinae. So it would seem that paternal care is not a cause for a small clutch size, but merely covaries with it.

Extremely precocial young are found in only one tribe, and therefore this effect can actually be a tribe effect. Thus there were three phylogeny-independent ecological factors influencing the reproductive traits:

distance from the equator, nest concealment and age at maturity.

Rate of development and egg size

The short incubation and fledging periods of arctic birds are clearly advantageous, as the breeding period is restricted. It can also be a strategy against nest predation, as most arctic breeders have exposed nests. As arctic waterfowl species have young that fledge relatively faster than those of more southern species, their young must either hatch at a more advanced stage or grow faster than those of other species.

Lack (1968) proposed that chicks hatching from large eggs are fatter or more advanced than those hatching from small eggs. Either of these conditions have been verified for different species (e.g. Ojanen 1983, Sotherland & Rahn 1987). In this study, large eggs — compared with the size of the species — were found in species with extremely precocial young (tribe Oxyurini) and those with arctic and temperate breeding ranges (Table 4 and 9). So it would seem that large eggs in ducks have evolved in order to produce young that are at an advanced stage at hatching or can attain flight rapidly, rather than fatter young. Fatter ducklings might be able to withstand cold better than light ducklings (Lack 1967), but cold-hardiness does not seem to be strongly connected with the relative egg size. I compared the relative egg size of ten species of northern ducks with their index of cold-hardiness, measured by Koskimies & Lahti (1964), but found no significant trend of cold-hardy species having larger eggs (Fig. 1). However, large eggs withstand cooling better than small eggs (Lack 1968, Kolbe 1979).

The longer relative incubation periods of hole-nesting species have been observed previously in ducks (Lack 1968) and passerines (Saether 1985). It has been suggested that as the nests of hole-nesting species are relatively safe from predators, it is more advantageous for the young of these species to spend more time as eggs than as ducklings (Lack 1968). However, the species with well-concealed nests on the ground had clutches as large for their size as hole-nesters, indicating that their nests are almost equally safe from predators. These species did not have a long incubation period, taking into account their size (Table 7). For their size, hole-nesters had larger clutch masses than open-nesting birds (Table 7). As clutch mass correlated positively with incubation period, hole-nesting species may have longer incubation periods simply because they have more to incubate.

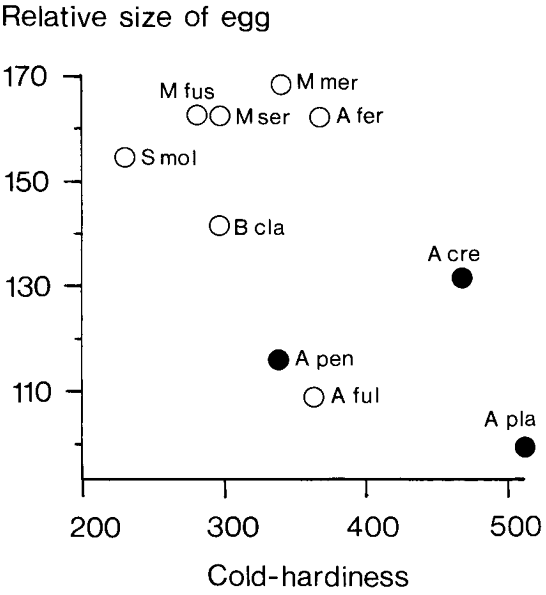

Fig. 1. The relationship of cold-hardiness (measured as metabolic effort of one-day-old ducklings at 10°C. Basic metabolic rate = 100. Species with low values are the cold-hardiest. Data from Koskimies and Lahti 1964) to relative egg weight (the effect of body weight removed, *Anas platyrhynchos* = 100). Solid dots indicate dabbling ducks, open dots sea ducks. Regression is not significant ($b = -0.183$, $F_s = 4.88$, $n = 10$).

Clutch size

Small clutches and clutch masses in late-maturing and also long-lived (Western & Ssemakula 1982) species, seem to depend on a universal trend of long-lived animals investing more in offspring quality than quantity (Williams 1966, Charnov & Krebs 1974, Wittenberger 1981).

Most Anatids lay one egg per day and start incubating after the last egg is laid. Predation is thought to limit large clutches as each egg lengthens the period the nest is vulnerable to predation (Perrins 1977). Although it has been argued that predation rates are too small to cause an evolutionary change in clutch size (Winkler & Walters 1983), my results are largely consistent with the hypothesis that predation is the main factor limiting the clutch size of species with poorly-concealed nests. Also, high rates of predation are reported in certain waterfowl studies (Choate 1967, Ahlén & Andersson 1970). Predation rates for ducks seem to be higher in the arctic, than in more southern regions (Swennen 1983). The small clutches of many arctic waterfowl species seem to depend

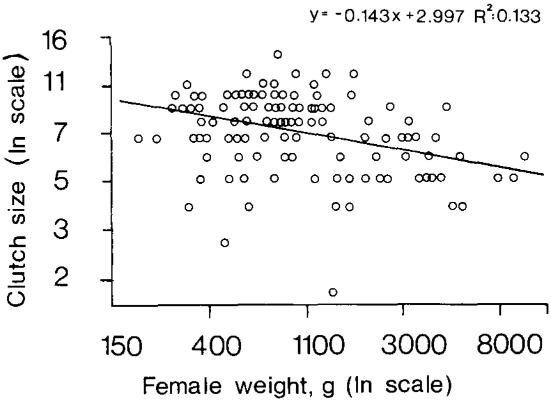

Fig. 2. The relationship between female weight and clutch size in Anatidae (both variables transformed with logarithms).

rather on the fact that nest predation is severe and that there are few hole-nesters in the arctic, than on the breeding latitude.

A central point in the clutch size determination in waterfowl has been Lack's proposal (1967, 1968) that clutch size is limited by the food resources available for the female prior to laying, and that these resources can be used to form many small, or a few large eggs. Thus a need for large eggs would be associated with small clutches. The results of my study do not support Lack's theory. Large eggs, in relation to the body size, were found in the tribe Oxyurini, with very precocial young, and in arctic and temperate species. Oxyurini species live in eutrophical lakes with an abundant food supply and they are known to lay replacement clutches, so despite the enormous eggs, the clutch size in this tribe seems not to depend on restricted food supply. Most arctic species with large eggs have clutches that total 20–30% of their body size (Johnsgard 1973), so it is doubtful that they could not lay larger clutches because of a limited food supply.

Are the reasons for evolving a small clutch likely to be the same in different species?

There is no absolute definition of a "small" clutch. If clutch size is plotted against female weight in the whole Anatidae, the largest waterfowl species of 10 kg are predicted to have a clutch size of five (Fig. 2). Thus at least all species weighing less than 10 kg, and with a clutch of five or less eggs, have clutches small for their size. Such small clutches are found in species of the tribes Oxyurini and Anserini, in all species of the genus Somateria — although it belongs to a tribe with a mean clutch size of eight (Mergini) — and in four dabbling duck species (here I have treated the Torrent Duck *Merganetta armata* and the Blue Duck *Hymenolaimus malacorhynchos* as dabbling ducks, although the former forms a tribe, and the latter a genus of its own, because of the proposed relationships between them and the other two Anatini species with very small clutches (Kear 1975, Johnsgard 1978)).

With the exception of the two most northern species, swans do not have clutches small for their size, but geese have. Swans and geese (Anserini) posses many factors connected with small clutches; they are large and late-maturing and they have poorly-concealed nests, prone to predation. The predation hypothesis is further supported by the fact that some species of arctic nesting geese incubate virtually without eating (Ankney & Mac Innes 1978, Johnsgard 1978), a behaviour which is also seen in eiders and believed to have evolved as a response to heavy nest predation (Milne 1976, Korschgen 1977).

Compared with the other species of the subfamily Anatinae, the stiff-tails (Oxyurini) show two aberrant features; they not only have clutches small for their size but also extremely large eggs and precocious young that can manage themselves when only a few days old (Lack 1968, Fjeldså 1977, Johnsgard 1978). The only true parasite among ducks is found in this tribe, and in almost all other species in this tribe dump-nesting is common. The relatively short incubation period, large eggs (capable of withstanding cooling) and very precocial young can be adaptations that minimize the costs of parasitism (Wittenberger 1981). Also, an obvious advantage of investing much energy in clutch, and little in brood rearing, would be to shorten the interval between two reproductive efforts. The Ruddy Duck *Oxyura jamaicensis* is indeed able to lay two clutches per breeding season in certain areas (Kolbe 1972, Palmer 1976), but all the other species lay only one clutch. However, with the exception of the Ruddy Duck, the other species of this tribe are rather poorly studied. The Musk Duck *Biziura lobata,* also belonging to this tribe, seems to have a different strategy. Musk Ducks lay only two eggs, and the female feeds her young, which are dependent on her even after fledging. This behaviour is suggested to limit the clutch size of this species (Johnsgard 1978).

Eiders are late-maturing, northern diving ducks, but so are all sea ducks (Mergini) and the only feature separating eiders from other Mergini species is that eiders have poorly-concealed nests, whereas almost all other Mergini species nest in holes or have well-concealed nests. Eiders also have short incubation periods for their size, but the fledging period or the time required for breeding is not shorter. This would support the hypothesis that the clutch size in this genus is limited by nest predation. As eiders incubate virtually without feeding (Korschgen 1977, Hario 1983), a short incubation period should be advantageous.

The four aberrant species of dabbling ducks (Torrent Duck, Blue Duck, Salvadori Duck *Anas waigiuensis* and Brown Teal *Anas aucklandica*) share certain features that are unusual among other dabbling ducks. They all have permanent pair-bonds and the males defend a territory and share in brood rearing (Johnsgard 1978). The breeding season is extended in at least the first three species, incubation and fledging periods are quite long and eggs large. At least for the Torrent Duck, an extremely long laying interval has been reported (Moffet 1970). Reduced growth rates and long laying intervals occur when food is scarce (Lack 1968), and territories are established to secure feeding or breeding sites (Wittenberger 1981). This could indicate that food is not very abundant for these species that feed in rapid, clear and well-oxygenated mountain streams (Torrent, Blue and Salvadori Ducks) or at the seashore (Brown Teal). The low food availability may perhaps limit clutch size directly, but more probably it has an indirect effect. The low food availability may necessitate a long laying interval and reduce clutch size, as the period between the laying of the first egg and the beginning of the incubation otherwise becomes too long. I must stress that this argument is quite hypothetical, as these species are all poorly studied. Also, the Brown Teal does not fit this idea very well.

It can, however, be concluded that — with the exception of species with similar breeding habits (geese and eiders) — the reasons for evolving a small clutch do not seem to be the same for different species.

Given the size, tribe and breeding latitude of a duck, its reproductive strategy is determined to a great extent. As reproductive traits scale allometrically to weight, it can be predicted that "adjustments in life-history evolve most rapidly through simple changes in size rather than in allometric proportions, since few gene loci would be involved in size shifts compared to scaling adjustments" (Western & Ssemakula 1982). Thus, a way to change a reproductive strategy would be to change the body size. Clutch size was the trait least determined by weight, phylogeny and breeding latitude and, thus, the only one which can be modified according to the different conditions a duck must cope with. Seen in this perspective it is hardly surprising that there was no single factor limiting clutch size in Anatidae and that these factors seemed to vary for different species. This also stresses that the possible ultimate factors affecting a trait should be studied separately for each species, as results obtained from one group (e.g. passerines or waterfowl) need not apply to other groups or species.

Acknowledgements. I am grateful to Esa Ranta for statistical advice, and to Olli Järvinen, Mikael Kilpi, Juha Tuomi, Kari Vepsäläinen and an anonymous referee for their comments on the manuscript. Financial support from the Finnish Cultural Foundation is greatly acknowledged.

Selostus: **Sorsalintujen lisääntymisstrategiat: ekologisten tekijöiden vai koon ja sukulaisuussuhteiden vaikutusta?**

Tutkin maailman sorsalintulajien lisääntymisstrategioiden kehittymiseen vaikuttaneita ekologisia tekijöitä, ts. yhdistääkö toisiaan muistuttavia lajeja jokin ekologinen tekijä (levinneisyysalue, etäisyys päiväntasaajasta, parisidos, ruokailutapa, sukukypsyysikä, pesän suojaisuus, koiraan osuus poikueen hoidossa, poikasten itsenäistymisikä), joka voisi olla strategian kehittymisen syy? Koska lajit voivat muistuttaa toisiaan myös siksi, että ne ovat samankokoisia tai toisilleen läheistä sukua, poistin ensin tilastollisesti koon vaikutuksen lisääntymisominaisuuksiin ja vertasin toisiinsa ekologisesti poikkeavia lähisukuisia lajeja. Aineisto koottiin käsikirjoista ja se käsitti 142 lajin lisääntymisominaisuuksia ja elintapoja koskevat tiedot (kaikkiaan lajeja on 149).

Kaikki tutkitut ominaisuudet korreloivat vahvasti lajin keskimääräisen painon kanssa (taulukko 3). Suurikokoisilla lajeilla oli suuremmat munat, pidempi haudonta-aika ja poikaskehitys sekä pienempi pesyekoko kuin pienikokoisilla.

Lajien koosta ja sukulaisuussuhteista riippumatta levinneisyysalueen pohjoisuus ja pesän avoimuus olivat yhteydessä poikasten kasvunopeuteen. Pohjoisilla lajeilla oli lyhyempi haudonta-aika ja nopeampi poikaskehitys kuin eteläisillä (taulukko 4). Tämä on ilmeisen edullista, koska pesimäkausi on lyhyt. Avopesijöillä oli lyhyempi haudonta-aika kuin kolopesijöillä (taulukko 7). Poikasten kehittyneisyys niiden kuoriutuessa oli yhteydessä munan kokoon. Pohjoisilla, nopeakasvuisilla lajeilla, ja lajeilla, joiden poikaset tulivat nopeasti vanhemmista riippumattomiksi, oli lajien kokoon nähden suuret munat (taulukko 4 ja 9). Avopesintä ja myöhäinen sukukypsyys olivat yhteydessä pieneen pesyekokoon (taulukko 5 ja 7). Lajit, jotka tulevat myöhään sukukypsiksi, ovat yleensä myös pitkäikäisiä. Ne lisääntyvät useita kertoja elämänsä aikana ja voivat saada vuotta kohti vähän jälkeläisiä. Pesärosvouksen uhka voi selittää, että avopesijöiden keskimääräinen pesyekoko oli pienempi kuin kolopesijöiden.

Pääkomponenttianalyysin perusteella suurin osa eri sorsalintulajien lisääntymisominaisuuksien välisistä eroista johtui lajien välisistä kokoeroista. Seuraavaksi tärkein tekijä oli levinneisyysalueen pohjoisuus, kolmas sukulaisuussuhteet (taul. 10). Yhteensä nämä tekijät selittivät 80–95% muiden ominaisuuksien, mutta vain 55% pesyekoon vaihtelusta lajien välillä (taulukko 11).

Yksi tapa lajin lisääntymisstrategian muuuttamiseen on muuttaa kokoa, koska kaikki lisääntymisominaisuudet korreloivat koon kanssa. Ehdotan, että tarvittava lisäsopeutuminen eri oloihin tapahtuu pesyekoon muutoksin, koska se on ominaisuuksista vähiten lajien koosta, perintötekijöistä ja pohjoisuudesta riippuvainen.

References

Ahlén, I. & Andersson, Å. 1970: Breeding ecology of an Eider population on Spitsbergen. — Ornis Scand. 1:83–106.

Ankney, C. D. & Mac Innes, C. D. 1978: Nutrient reserves and reproductive performance of female Lesser Snow geese. — Auk 95:459–471.

Bauer, K. M. & Glutz von Blotzheim, U. N. 1968–1969: Handbuch der Vögel Mitteleuropas. Band 2 and 3. — Akademische Verlagsgesellschaft, Frankfurt.

Bezzel, E. 1985: Kompendium der Vögel Mitteleuropas: Nonpasseriformes — Nichtsingvögel. — AULA, Wiesbaden.

Blueweiss, L., Fox, H., Kudzma, V., Nakashima, D., Peters, R. & Sams, S. 1978: Relationships between body size and some life-history parameters. — Oecologia (Berl.) 37:257–272.

Brown, L. H., Urban, E. K. & Newman, K. 1982: The birds of Africa. Vol. 1. — Academic Press, London.

Charnov, E. L. & Krebs, J. R. 1974: On clutch size and fitness. — Ibis 116:217–219.

Choate, J. S. 1967: Factors influencing nesting success of eiders in Penobscot Bay, Maine. — J. Wildlife Manage. 31:769–777.

Cramp, S. (ed.) 1977: Handbook of the birds of Europe, the Middle East and North Africa. The birds of the Western Palearctic. Vol. 1. Ostrich to Ducks. — Oxford University Press, Oxford.

Delacour, J. 1954–59: The waterfowl of the world. — Country Life. London.

Elgar, M. A. & Harvey, P. H. 1987: Basal metabolic rates in mammals: allometry, phylogeny and ecology. — Functional Ecology 1:25–36.

Fjeldså, J. 1977: Guide to the young of European precocial birds. — Skarv Nature Publications.

Frith, H. J. (ed.) 1983: Complete book of Australian birds. — Reader's Digest Services, Sydney.

Goodman, D. 1974: Natural selection and a cost ceiling on reproductive effort. — Am. Nat. 108:247–268.

Hario, M. 1983: Haahkanaaraan haudonta-aikainen painonkehitys. (Summary: Weight loss of incubating female eiders). — Suomen Riista 30:28–33.

Johnsgard, P. A. 1965: Handbook of waterfowl behaviour. — Cornell Univ. Press, Ithaca.

Johnsgard, P. A. 1973: Proximate and ultimate determinants of clutch size in Anatidae. — Wildfowl 24:144–149.

Johnsgard, P. A. 1978: Ducks, geese and swans of the world. — Univ. Nebraska Press, Lincoln.

Kear, J. 1975: Salvadori's duck of New Guinea. — Wildfowl 26:104–111.

Kendeigh, S. C. 1969: Tolerance of cold and Bergmann's rule. — Auk 86:13–25.

Klomp, H. 1970: The determination of clutch size in birds: a review. — Ardea 58:1–124.

Kolbe, H. 1972: Die Entenvögel der Welt. — Neumann Verlag, Radebeul.

Kolbe, H. 1979: Ornamental Waterfowl. — Gresham Books, Surrey.

Korschgen, C. E. 1977: Breeding stress of female Eiders in Maine. — J. Wildl. Manage. 41:360–373.

Koskimies, J. & Lahti, L. 1964: Cold-hardiness of the newly hatched young in relation to ecology and distribution in ten species of european ducks. — Auk 81:281–307.

Lack, D. 1967: The significance of clutch-size in waterfowl. — Wildfowl Trust Ann. Rep. 18:125–128.

Lack, D. 1968: Ecological adaptations of breeding in birds. — Methuen, London.

Milne, H. 1976: Body weights and carcass composition of the Common Eider. — Wildfowl 27:115–122.

Moffet, G. M. 1970: A study of nesting torrent ducks in the Andes. — Living Bird 9:5–28.

Ojanen, M. 1983: Significance of variation in egg traits in birds, with special reference to passerines. — Acta Univ. Ouluensis. A 154. Biologica 20. 49+46 pp.

Palmer, R. S. (ed.) 1976: Handbook of North American birds. Vols. 2 and 3. — Yale Univ. Press, New Haven.

Perrins, C. M. 1977: The role of predation in the evolution of clutch size. — In: Stonehouse, B. & Perrins, C. M. (eds.), Evolutionary Ecology, pp. 181–191. Macmillan Press, Surrey.

Rahn, H., Paganelli, C. V. & Ar, A. 1975: Relation of avian egg weight to body weight. — Auk 92:750–756.

Saether, B. E. 1985: Variation in reproductive traits in European passerines in relation to nesting site: allometric scaling to body weight or adaptive variation? — Oecologia (Berl.) 68:7–9.

Saether, B. E. 1987: The influence of body weight on the covariation between reproductive traits in European birds. — Oikos 48:79–88.

Schaffer, W. M. 1974: Selection for optimal life-histories: the effects of age structure. — Ecology 55:291–303.

Sokal, R. R. & Rohlf, F. J. 1981: Biometry. 2nd ed. — Freeman and co, New York.

Sotherland, P. R. & Rahn, H. 1987: On the composition of bird eggs. — Condor 89:48–65.

Stearns, S. C. 1983: The influence of size and phylogeny on patterns of covariation among life-history traits in mammals. — Oikos 41:173–187.

Swennen, C. 1983: Reproductive output of Eiders Somateria mollissima mollissima on the southern border of its breeding range. — Ardea 71:245–254.

Tuomi, J., Hakala, T. & Haukioja, E. 1983: Alternative concepts of reproductive effort, costs of reproduction, and selection in life-history evolution. — Amer. Zool. 23:25–34.

Wanntorp, H.-E. 1983: Historical constraints in adaptation theory: traits and non-traits. — Oikos 41:157–159.

Western, D. & Ssemakula, J. 1982: Life-history patterns in birds and mammals and their evolutionary interpretation. — Oecologia (Berl) 54:281–290.

Williams, G. C. 1966: Natural selection, the costs of reproduction and a refinement of Lack's principle. — Am. Nat 100:687–690.

Winkler, D. W. & Walters, J. R. 1983: The determination of clutch size in precocial birds. — In: Johnston, R. F. (ed.), Current Ornithology. Vol. 1, pp. 33–68. Plenum, New York.

Wittenberger, J. F. 1981: Animal social behaviour. — Duxbury Press, Boston.

Received 3 November 1987, accepted 29 December 1987

Instructions to authors

ORNIS FENNICA is published quarterly and contains scientific ornithological articles. The contents may be descriptive, experimental or theoretical, in the form of research reports or reviews. Connections with Finnish or Scandinavian ornithological research are desirable, but papers of broad general interest are also accepted. Contributions are welcomed from all parts of the world, but should be written in English (in exceptional cases other languages may be accepted).

Manuscripts should be submitted to the Editors (see inside front cover) **in three copies**, including tables and figures and their captions (on separate pages). All typewritten material should be double-spaced on one side of good quality paper with at least 3 cm margins. If the manuscript is written on a word processor, please inform the Editors, because it may be possible to print the text directly from the processor disc.

The *format* of the manuscript (title, headings, abstract, references, tables, etc.) should be in accordance with recent issues of the journal. For italics use underlining. Do not divide words. Do not use boldface, right margin justification, or other special word processor features. Both scientific and vernacular names should be given when birds are first mentioned in the text. Use the 24-hour clock (e.g. 09.00 and 22.30) and dates as 1 April 1987. The abstract should not exceed 175 words.

In the list of *references* the following format should be used:

Angelstam, P. K., Jaarola, M. & Nordh, N.-E. 1985: Are female Black Grouse Tetrao tetrix territorial? — Ornis Fennica 62:1–9.

Calder, W. A. 1974: Consequences of body size for avian energetics. — In: Paynter, R. A. (ed.), Avian energetics, pp. 86–115. Nuttall Ornithol. Club, Cambrigde, Mass.

Pielou, E. C. 1974: Population and community ecology. Principles and methods. — Gordon & Breach, New York.

Journal names should be abbreviated as in Biol. Abstr.; if in doubt, do not abbreviate. Do not use italics in references. Do not cite papers in preparation.

Tables should be comprehensible without reference to the text. Avoid long column headings, complicated structure and vertical lines. Plan your tables for column or page width.

All *illustrations* should be numbered consecutively as figures. Parts of figures should be identified with letters, not numbers (e.g. Fig. 1A). Plan your figures for column or page width when printed. Typewritten lettering is not acceptable. Lettering should be large enough to be readable after reduction of the figure and the lettering style must be uniform in all figures. The figures may be submitted as originals or as glossy prints (please note that figures larger than A4 are easily damaged in the mail). Photographs should have good contrast and be sharp.

The *statistical methods* used should be adequately documented. Means and percentages should usually be given with standard deviations (SD) and the numbers of observations (n). Numerical values of test statistics (including nonsignificant values) should usually be given along with their degrees of freedom (df) and probabilities (P). Give probabilities either as, e.g., $P<0.05$ or exactly. When reporting X^2- or G-tests, total n must be clearly indicated.

Refereeing. All manuscripts within the scope of the journal will be reviewed by at least two referees. Authors will generally be notified of acceptance or rejection within two months.

Proofs. Authors will receive proofs for approval. Extensive alterations will be charged to the author.

Reprints. Authors will receive 50 reprints free of charge; additional copies can be obtained at cost price.