Reproductive Characteristics of Meadow Birds and Other European Waders

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Introduction

Altogether over 50 wader species occur in Western Europe (Glutz *et al.*, 1975, 1977). Eight of these: Dunlin *Calidris alpina*, Ruff *Philomachus pugnax*, Common Snipe *Gallinago gallinago*, Redshank *Tringa totanus*, Lapwing *Vanellus vanellus*, Black-tailed Godwit *Limosa limosa*, Oystercatcher *Haematopus ostralegus* and Curlew *Numenius arquata* can be found regularly nesting in wet meadows. These species are from now on called meadow birds.

The meadow birds can be divided into two categories: Dunlin, Ruff, Common Snipe and Redshank are considered as 'vulnerable species', whereas Lapwing, Black-tailed Godwit, Oystercatcher and Curlew are considered as 'non-vulnerable' (Beintema 1983, this volume). This distinction is based on the species' response to intensification of agricultural grassland use, which causes a general decline in the vulnerable species.

In this paper we will investigate whether there are differences in the breeding biology of the meadow birds as compared to the other wader species in Western Europe, and whether there are differences between the "vulnerable" and the 'non-vulnerable' species. All basic information is presented in Table 1.

Adult size

The adult weights listed in Table 1 refer to the female weights during the incubation period. As can be seen from Figure 1, the meadow birds are underrepresented in the species weighing up to 100 g.

The average weights for females of the vulnerable and non-vulnerable species are 101 g (s.e.=21) and 468 g (s.e.=144), respectively.

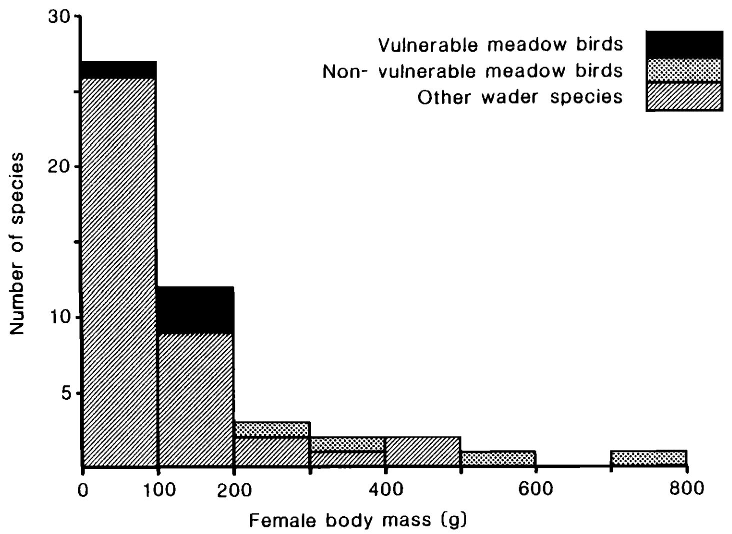

Figure 1. Frequency distribution of female weights of vulnerable meadow birds, non-vulnerable meadow birds, and other European waders.

Table 1. Reproductive parameters of European waders

	female weight (g)	egg weight (g)	neonate weight (g)	number of eggs	incubation period (days)	asympt. mass (g)	maximal growth (g/day)	source*
vulnerable meadow birds								
Calidris alpina	50	10.1	7.0	4	21	50	2.0	
Philomachus pugnax	110	21.5	13.5	4	21	168	5.4	
Gallinago gallinago	110	16.4	11.3	4	20	111	4.5	1
Tringa totanus	135	22.3	15.0	4	24	137	3.5	
non-vulnerable meadow birds								
Vanellus vanellus	230	26.0	17.0	4	27	236	4.7	
Limosa limosa	316	40.5	28.6	4	23	273	8.5	2
Haematopus ostralegus	536	47.0	30.4	3	27	466	13.9	3
Numenius arquata	788	76.0	56.6	4	28	990	18.6	
other European species								
Himantopus himantopus	169	21.8	-	4	23	-	-	
Recurvirostra avosetta	274	32.3	21.3	4	24	-	-	
Burhinus oedicnemus	449	38.9	-	2	25	-	-	
Pluvialis apricaria	176	31.4	22.6	4	31	261	5.7	
Pluvialis dominica	146	26.0	18.4	4	26	-	-	
Pluvialis squatarola	189	34.2	-	4	27	-	-	
Charadrius hiaticula	65	11.5	8.1	4	24	61	2.3	
Charadrius dubius	39	7.5	5.3	4	25	41	1.5	
Charadrius alexandrinus	47	9.1	6.4	3	26	47	1.2	4
Charadrius mongolus	63	12.0	-	3	23	-	-	
Charadrius leschenaultii	90	14.7	11.6	3	-	-	-	
Charadrius asiaticus	75	13.8	-	3	-	-	-	
Eudromias morinellus	117	17.0	11.5	3	26	111	4.8	
Limosa lapponica	320	37.0	-	4	21	-	-	
Numenius phaeopus	450	51.0	41.0	4	28	360	11.0	5
Bartramia longicauda	164	25.2	17.0	4	25	-	-	
Tringa stagnatilis	78	14.0	-	4	-	-	-	
Tringa nebularia	175	30.5	-	4	24	-	-	
Tringa flavipes	84	17.5	-	4	23	-	-	
Tringa ochropus	85	15.5	-	4	20	-	-	
Tringa glareola	62	13.5	-	4	22	-	-	
Xenus cinereus	74	13.2	-	4	21	-	-	
Actitis hypoleucos	55	12.8	9.0	4	21	-	-	
Arenaria interpres	118	17.0	12.2	4	22	-	-	
Phalaropus tricolor	68	9.4	6.6	4	20	-	-	
Phalaropus lobatus	35	6.3	3.9	4	18	-	-	
Phalaropus fulicarius	61	8.8	5.3	4	19	-	-	
Scolopax rusticola	280	24.5	18.0	4	22	-	-	
Calidris canutus	148	19.3	11.0	4	22	-	-	
Calidris alba	57	11.2	7.3	4	25	81	2.5	
Calidris pusilla	29	7.3	-	4	19	26	1.4	
Calidris ruficollis	29	8.0	5.7	4	-	-	-	
Calidris minuta	31	6.3	-	4	-	-	-	
Calidris temminckii	26	6.0	4.3	8	21	-	-	
Calidris fusicollis	46	9.8	5.0	4	22	37	2.2	
Calidris bairdii	39	10.1	6.6	4	20	48	2.1	
Calidris melanotus	63	12.9	-	4	-	60	2.3	
Calidris maritima	80	13.3	9.0	4	22	-	-	
Calidris ferruginea	63	12.0	7.7	4	-	-	-	
Tryngites subruficollis	53	12.5	-	4	-	-	-	

*sources: 1. Green (1985); 2. J.E. Winkelman unpubl. data; 3. Drent & Klaassen (1989); 4. T. Szekely unpubl. data; 5. M. Grant unpubl. data; all other data Glutz v. Blotzheim *et al.* (1975 and 1977); Beintema & Visser (1989b).

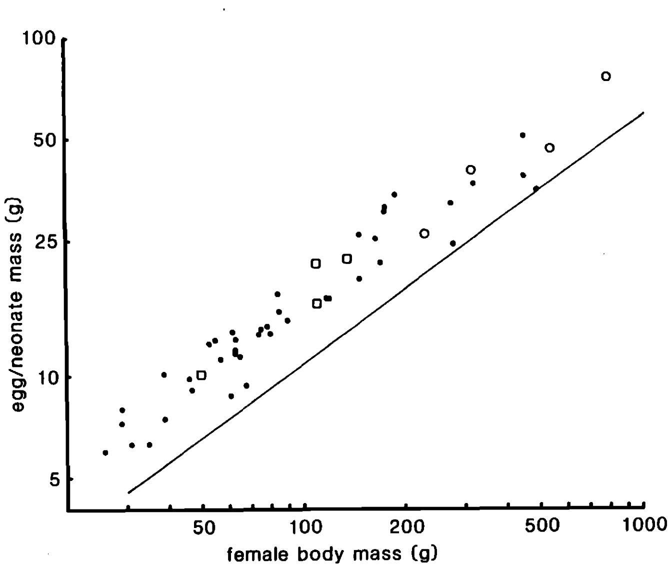

Figure 2. Egg weight as a function of female body weight in vulnerable (open squares), non-vulnerable (open circles) meadow birds, and other European waders (dots). The drawn line is the regression line for the weight of the neonate as a function of female weight.

Basal metabolic rate and daily energy budget of the adults

No detailed studies on the energetics during the reproductive period are available for meadow birds. Kersten & Piersma (1987) made a compilation of basal metabolic rates in waders. Their formula (BMR=5.06(body weight)$^{0.729}$, body weight in kg, BMR in watts) suggests a strong effect of the weight on the BMR. They also concluded that the daily energy budget and BMR are closely linked (DEB = 3xBMR). Therefore we may assume that the daily energy intake for the smaller vulnerable meadow birds is lower than for the larger, non-vulnerable species. These formulae do not however tell us how difficult it is to match food intake and daily energy budget for a given species. We need more information on the time and energy budgets for both vulnerable and non-vulnerable meadow bird species.

Female size and egg-size

The regression between female body weight and egg weight (between species) is given in Figure 2. As can be seen, heavy females do produce large eggs. The regressions for meadow birds and the other waders do not differ significantly. The formula for all waders is:

egg weight = 0.652 (female weight)$^{0.702}$,r=0.97, n = 48; egg and female weights in grams.

For a typical wader of 250 g the egg size is 31.4 g. For a galliform and an anseriform bird of the same size the egg weights are 16.6 g and

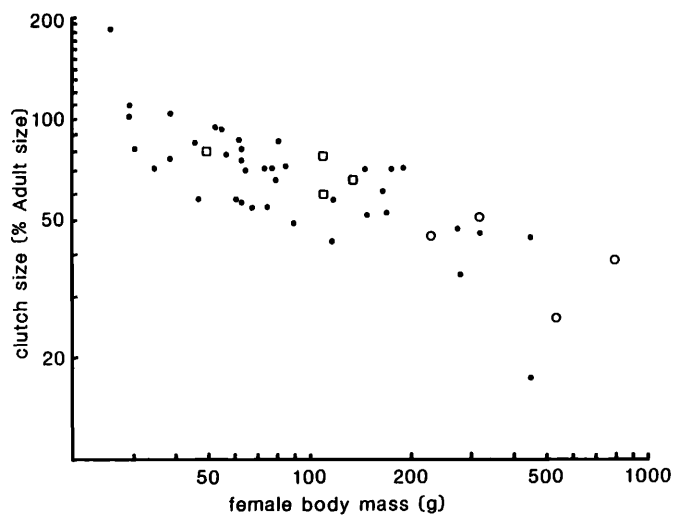

Figure 3. Relative clutch weight as a function of female weight in vulnerable (open squares), non-vulnerable (open circles) meadow birds, and other European waders (dots).

26.3 g respectively (Rahn *et al.* 1975).

The average egg weights for the vulnerable and non-vulnerable species are 17.6 g (s.e. = 3.2) and 47.4 g (s.e. = 12.1), respectively.

In Figure 2 we also show the relation between female body weight and hatchling weight:

hatchling weight = 0.377(female weight)$^{0.733}$, r=0.96, n = 34; hatchling and female weights in grams.

When we express clutch size relative to body weight, small species tend to produce heavy clutches (Figure 3) in comparison to large species. In some cases the weight of the clutch equals the body weight of the female. This may put a strain on the costs of egg formation and incubation, and may reduce the possibility of producing a replacement clutch in the case of nest loss.

The averages for relative clutch size for vulnerable and non- vulnerable species are 71.2 % (s.e. = 5.8) and 40.4 % (s.e. = 6.2), respectively.

Egg size and incubation period

Figure 4 gives the relationship between egg weight and incubation period. In general, larger eggs have longer incubation periods than smaller ones, although the variation is considerable. No significant difference could be detected between the meadow birds and the other waders. The general formula for waders is:

incubation period = 16.1 (egg weight)$^{0.125}$, r = 0.63, n = 40; incubation period in days, egg weight in grams.

For the vulnerable and non-vulnerable meadow bird species the incubation periods are 22 (s.e.= 0.8) and 26.3 (s.e.= 1.3) days respectively.

Long incubation periods seem to be disadvantageous because of the risk of predation. If the probability that a clutch will survive one day is P (P = daily survival rate), the probability H that a clutch will hatch, can be calculated as $H = P^n$, where n is length of the incubation period, in days. Thus, for a given daily survival rate, the probability of surviving until hatching is smaller for a clutch of large eggs than for one with small eggs.

Neonate size and development of thermoregulation

Figure 5 shows a semilogarithmic relation between neonate weight and the index of homeothermy (Visser & Ricklefs, in prep.). No difference could be detected between meadow

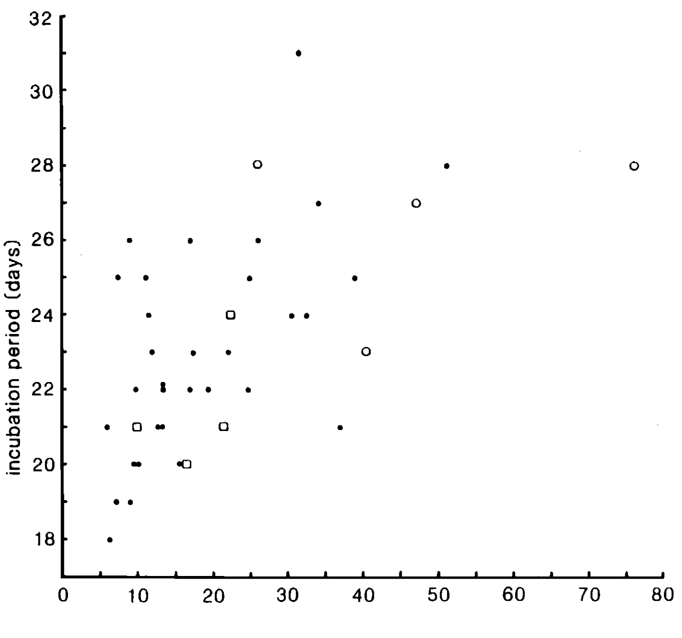

Figure 4. Incubation period as a function of fresh egg mass in vulnerable (open squares), non-vulnerable (open circles) meadow birds, and other European waders (dots).

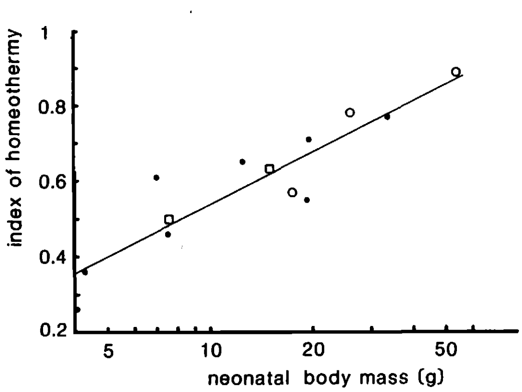

Figure 5. Index of homeothermy as a function of hatchling weight in vulnerable (open squares), non-vulnerable (open circles) meadow birds, and other European waders (dots). The index of homeothermy is defined as (tbf-ta)/(tbi-ta), where tbf and tbi stand for the chick's final (after 30-minute cold exposures) and initial body temperature, respectively, and ta is the ambient temperature (18°C).

birds and the other waders. The general formula is:

H = 0.464 ($\log_{10}$ neonate weight) + 0.07; r = 0.91, n = 13; neonate weight in grams.

According to the formula heavier neonates are more homeothermic than the smaller ones.

In most wader species, chicks have to find their own food. At low ambient temperatures the chicks cannot maintain their body temperature, and need to be brooded regularly by a parent. The time the chicks spend being brooded is lost for feeding activities. Beintema & Visser (1989a) found a positive correlation between the percentage of time available for foraging and the daily weight gain in small chicks of Lapwings and Black-tailed Godwit. Because heavier neonates have a higher degree of homeothermy than the smaller ones, heavy chicks have more time available for foraging, and may grow faster.

Chick size and growth rate

Figure 6 illustrates the relationship between the asymptotic weight of a chick, and its maximum growth rate in the inflection point, according to Gompertz' equation (calculated from Beintema & Visser 1989b). Large species do have high absolute growth rates. No difference could be detected between the meadow birds and the other waders. The formula for all waders is:

max. growth = 0.104 (asympt. weight)$^{0.76}$, r = 0.96, n = 19; asymptotic weight in grams, maximum growth rate in grams/day.

For the vulnerable and non-vulnerable species the averages are 3.6 (s.e.= 0.6) and 11.4 (s.e.= 3.5) grams/day respectively.

The constant (0.104) for waders is much lower than for altricial species (0.202) according to Drent & Daan (1980). Precocial species do have a higher energy expenditure with respect to locomotion and thermoregulation than altricial species, and therefore less energy is retained for growth.

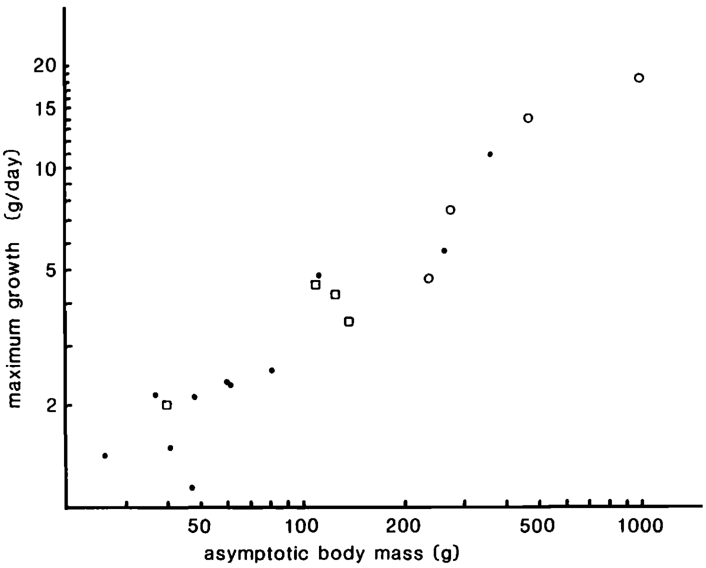

Figure 6. Maximum weight gain in the inflection point as a function of asymptotic mass in vulnerable (open squares), non-vulnerable (open circles) meadow birds, and other European waders (dots).

From laboratory experiments, Beintema *et al.* (1991) have calculated a daily consumption prior to fledging of 14,000, 18,000, 22,000 and 42,000 insects each of 1 milligram dry weight for Redshank, Lapwing, Black-tailed Godwit and Curlew respectively.

Chicks from the non-vulnerable species seem to have much higher food intake than chicks of the vulnerable species (and have to rely more on larger prey items).

The length of the fledging periods of wader chicks is reviewed by Beintema & Visser (1989b). Smaller hatchlings have shorter fledging periods as compared to the larger ones. The total time span between the onset of laying and fledging of the chicks amounts to up to 50 days in all vulnerable species and the Black-tailed Godwit, and up to 65 days in the other non-vulnerable species.

Conclusions

With respect to the egg size versus female weight, incubation period versus egg weight, degree of homeothermy versus hatchling weight and growth rates versus asymptotic weight, no significant differences could be detected between the meadow birds and other European waders. In general meadow birds are large in comparison to the other European waders, and the larger meadow bird species are less vulnerable than the smaller ones. We need more studies on time and energy budgets of adults and chicks of vulnerable and non-vulnerable species to fully understand the process of meadowbirdification.

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