COMPONENTS OF FITNESS IN LAPWINGS *VANELLUS VANELLUS* AND BLACK-TAILED GODWITS *LIMOSA LIMOSA* DURING THE BREEDING SEASON: DO FEMALE BODY MASS AND EGG SIZE MATTER?

ZOLTÁN HEGYI & LAJOS SASVÁRI

Hegyi Z. & L. Sasvári 1998. Components of fitness in Lapwings *Vanellus vanellus* and Black-tailed Godwits *Limosa limosa* during the breeding season: do female body mass and egg size matter? Ardea 86:43-50.

Body mass of incubating females, their egg sizes, hatching success, hatchling masses and brood survival were recorded for individually colour-marked Lapwings *Vanellus vanellus* and Black-tailed Godwits *Limosa limosa* breeding on meadows in Kiskunság National Park, 50 km south of Budapest, Hungary. We found no relationships between egg size and body mass of females, but there were positive correlations between female body mass and hatching success in both species. Laying date did not effect hatching success. Females replaced a clutch only if the first clutch was destroyed during the first half of incubation. Females that laid replacement clutches were heavier at the start of incubation of their first clutches than females that did not relay. The longest time interval, and the greatest nest distance, between first and replacement clutches were respectively 17 days and 94 m in Lapwings, and 20 days and 120 m in Black-tailed Godwits. Egg sizes were smaller in replacement clutches than in first clutches. Egg size was positively correlated with hatchling mass and with brood survival in both species, but brood survival decreased with hatching date. Females tending the chicks together with their mates suffered fewer chick losses before fledging than lone females.

Key words: *Vanellus vanellus* - *Limosa limosa* - parental investment - breeding success - waders - maternal body condition - replacement clutches - precocial chick mass

Department of General Zoology, Eötvös University, Pf/330, Puskin u. 3, H-1445 Budapest, Hungary, E-mail: sasvari@abc.hu

INTRODUCTION

Egg size may indicate egg quality and the likelihood that a chick survives. Egg size has been correlated with hatchling mass and size, growth rate, fledgling mass and chick survival in cormorants (Amundsen & Stokland 1990), grouse (Moss *et al.* 1981), auks (Birkhead & Nettleship 1982), skuas (Furness 1983), gulls (Parsons 1970; Lundberg & Väisänen 1979; Bolton 1991), terns (Nisbet 1978) and tits (Schifferli 1973). Nice (1937) was the first to draw attention to a relationship between female size and egg size. Positive as well as negative correlations have since been reported (Anderson *et al.* 1970; Murton *et al.* 1974; Myrberget 1977; Murphy 1978; Miller 1979; Ojanen *et al.* 1979; Otto 1979; Järvinen 1991; versus Labisky & Jackson 1969; Ankney & Bisset 1976; Batt & Prince 1978; De Steven 1978). Galbraith (1988) and Grant (1991) showed that in waders clutch survival may depend on egg size, and thus perhaps on female size. Nevertheless, in his review, Williams (1994) showed that studies on the relationships between egg size and chick survival are limited to the early-chick stage; good evidence regarding these relationships is sparse. Beintema & Visser (1989) compared fledging periods among wader species and found that sandpipers (Scolopacidae) grow faster than plovers (Charadriidae).

In this study of a plover (the Lapwing *Vanellus vanellus*), and a sandpiper species (the Black-tailed Godwit *Limosa limosa*), we investigated the relationships between female body mass on the one hand, and (possible) components of fitness such as egg size, hatchling mass and chick survival on the other. As we worked with individually marked females, we were able to focus on any replacement clutches when first clutches were destroyed.

METHODS

The 380 ha study area in Kiskunság National Park 50 km south of Budapest (47°08'N, 19°07'E) was a site where artificial fish ponds were created in 1953. Fish-breeding was abandoned in 1966 so the ponds dried up, but in 1987 they were flooded again for the first time. During the study years 1988-1995 the ponds dried up each August and were re-flooded every autumn. No water management or agricultural activities took place during the breeding season. A meadow of 210-240 ha provided suitable breeding habitat, with the rest of the area being under water.

Nests were detected by locating incubating parents either from a car parked on the banks of the ponds or from hides. About 70-80 ha could be viewed from the hides and 130-160 ha from cars on the banks. Nests were mapped and marked with sticks placed a few meters away. Nest searches started in early March at 3-4 day intervals. Once found, nests were checked every 3-4 days. When the first egg-laying, hatching or any event within the clutch occurred during the period between two checks, the day halfway between visits was recorded. After the eggs hatched, an 2 km wide strip surrounding the study site was also surveyed.

Birds were colour-marked using the technique suggested by Paton & Pank (1986). Dummy eggs were treated with a mixture of oil jelly and either Rhodamin B, anilin blue or xylinene orange. Beads of gel (5-10 mm by 3-5 mm) were placed along the length of the eggs, which were then placed in nests. Combinations of the colours marked the individuals in unique patterns on their abdomens and breasts so that they could be individually identified. Sexes were identified on the basis of display and copulatory behaviour.

Nest losses resulting from predation were identified by their complete disappearance before the expected time of hatching, or by the presence of partially eaten eggs in or near the nest. All losses not resulting from predation were considered due to 'other disturbances' which includes flooding following rainfall. When the chicks were 10-15 days old, and when they should have been 25-30 days old, we recorded presence or absence of their mothers. If females were guarding, part of their broods was considered to be alive. When mothers of chicks less than 30 days old disappeared the brood was considered unsuccessful. In one Lapwing family and three Black-tailed Godwit families, males tended chicks alone because the females deserted. These cases were omitted from the analyses.

For each egg maximum length (L) and breadth (B) were measured, and egg volume (V) was calculated using the formula, $V = 0.51LB^2$ (Hoyt 1979). The masses of freshly laid eggs (weighed within two days after laying) and fresh hatchlings were weighed with Pesola spring balances. Egg sizes and hatchling masses were averaged for each clutch and the mean used for further calculations. Adult females were weighed on electronic balances (± 1 g) set below nests. Balances were placed in a pit below the nests and taken out after each measurement. Displays connected with the balance were read from the car or the hide. Balances were calibrated using known weights each time measurements were made.

Statistical analyses were carried out using SPSS. Logistic regression was used to model clutch survival and brood survival (Cox & Snell 1989). Multiple logistic regression was used to model effects of laying date, female mass and egg size on clutch survival and hatching date, hatchling mass and female status (lone or with a mate) on brood survival. We calculated the maximized log-likelihood multiplied by a factor of 2 for deviance, and showed the difference in deviance χ^2-tests.

RESULTS

Sixty-seven female Lapwings and 65 female Black-tailed Godwits were individually marked. Sixty Lapwings (89.6%) and 60 Black-tailed Godwits (92.3%) laid clutch of four eggs; the others laid three eggs. Body masses of 64 female Lapwings and 57 female Black-tailed Godwits were measured during the first week of incubation. There were no significant correlations between body mass and mean egg volumes for first clutches (r_{64} = 0.213, n.s., and r_{57} = 0.106, n.s.). The mean (± SD) body masses and egg volumes for Lapwings were 197.3 ± 16.5 g and 25.03 ± 2.63 cm^3 and for Black-tailed Godwits 286.4 ± 21.6 g and 45.28 ± 8.10 cm^3. We weighed freshly laid eggs in the first clutches of 32 Lapwings and 31 Black-tailed Godwits and found no significant correlations between egg masses and maternal body mass (r_{32} = 0.162, n.s., and r_{31} = 0.219, n.s., respectively). The mean egg masses for Lapwings were 24.33 ± 2.71 g and 36.87 ± 4.54 g for Black-tailed Godwits.

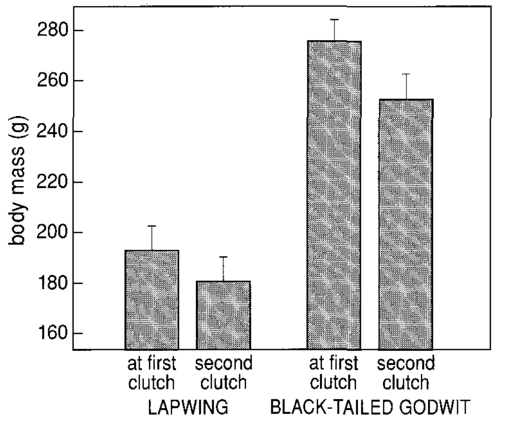

Fig. 1. Body mass of female Lapwings and Black-tailed Godwit (mean with vertical lines indicating SE, *n*= 14 for either species) in the early incubation period of the first (left column) and replacement clutches (right column). See text for statistics.

Twenty-five Lapwings and 31 Black-tailed Godwits of the weighed sample lost their first clutches, with 14 females of each species laying a replacement clutch in the study area. Body mass

Table 1. Egg size in first and replacement clutches and the body mass (g) of female Lapwings and Black-tailed Godwits in the first week of incubation that either or not replaced lost clutches.

		Lapwing			Black-tailed Godwit		
	clutch	*n*		SD	*n*		SD
Egg volumes (cm^3)	first	14	24.71	1.03	14	45.37	1.30
	replacement	14	23.82	1.37	14	44.21	1.10
Egg mass (g)	first	9	25.72	2.03	7	41.81	4.22
	replacement	9	21.60	1.56	7	36.70	2.97
Female mass (g)	replaced first clutch	14	191.0	11.7	14	275.5	12.2
	did not replace first clutch	5	160.6	9.4	13	262.2	10.8

Table 2. Logistic regression models for clutch survival: effects of laying date, body mass of female Lapwings and Black-tailed Godwits in the first week of incubation and egg volume. Clutch survival was calculated on first clutches incubated/destroyed in the early incubation period (until 15th day after last egg was laid) and hatched/destroyed in the late incubation period (after 15th day of incubation). Laying date was calculated with 1 denoting the date when the first egg of the first clutch was recorded during a given breeding year and increased with the number of days in that particular year. Egg volumes were averaged for each clutch and mean was used for calculation.

			Regression coefficients		
	χ^2	*df*	*P*-value	*B*	SE of *B*
Lapwing (n= 64)					
Laying date	2.52	1	0.123	0.013	0.026
Body mass of female	4.80	1	0.031	0.039	0.011
Egg volume	1.74	1	0.192	0.009	0.004
Black-tailed Godwit (n= 57)					
Laying date	2.60	1	0.117	0.016	0.024
Body mass of female	5.16	1	0.028	0.042	0.013
Egg volume	2.06	1	0.087	0.011	0.025

Table 3. Logistic regression models for brood survival during the chick-rearing period in Lapwings and Black-tailed Godwits: effects of hatching date, hatchling mass and female status. Brood survival was calculated on the presence/absence of female which guarded chicks when they were 10-15 days old or when they should have been 25-30 days old. Hatching date was calculated with 1 denoting the date when the first egg of the first clutch hatched during a given breeding year and increased with the number of days in that year. Hatchling masses were averaged for each brood and mean was used for calculation. Female status was calculated for females that guarded relatively young and old chicks alone or with their mates.

			Regression coefficients		
	χ^2	*df*	*P*-value	*B*	SE of *B*
Lapwing (n= 25)					
Hatching date	5.18	1	0.028	-0.041	0.013
Hatchling mass	8.06	1	0.009	0.035	0.019
Female alone/with mate	6.07	1	0.015	0.029	0.007
Black-tailed Godwit (n= 21)					
Laying date	6.03	1	0.018	-0.032	0.009
Hatchling mass	7.53	1	0.012	0.026	0.011
Female alone/with mate	5.91	1	0.018	0.024	0.006

of these females was measured again at the start of incubation of replacement clutches. Females lost mass between the early incubation period of the first clutch and the early incubation period of replacement clutch (Student's t-tests for Lapwing, t_1 = 3.14, P < 0.01; for Black-tailed Godwit, t_1 = 2.56, P < 0.05; Fig. 1). No significant correlations were found between the body mass and egg volume in replacement clutches of either species (Lapwing r_{14} = 0.166, n.s.; Black-tailed Godwit

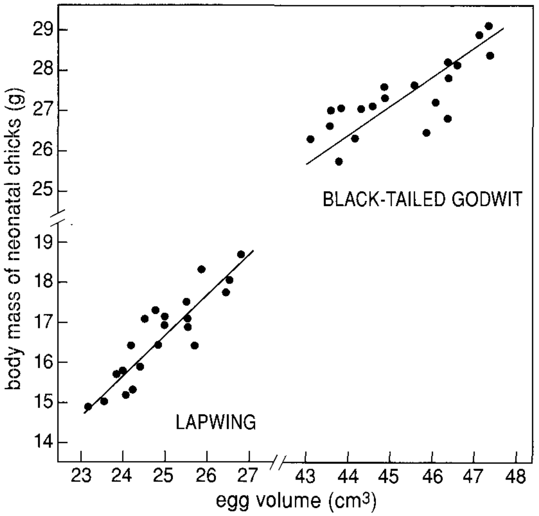

Fig. 2. Relationships between egg volume and neonatal chick mass in Lapwings and Black-tailed Godwits in Hungary. See text for statistics.

r_{14} = 0.385, n.s.). For both Lapwings and Black-tailed Godwits egg volume was smaller in replacement clutches than in first clutches (Table 1; t_1 = 2.22, $P < 0.05$ and t_1 = 2.58, $P < 0.02$, respectively), as were the masses of freshly laid eggs (t_1 = 2.44, $P < 0.05$ and $t_1 = 2.97$, $P < 0.05$). Females that laid replacement clutches were heavier during early incubation of the first clutch than females that did not relay (Table 1; Lapwing $t_1 = 5.80$, $P <$ 0.001; Black-tailed Godwit $t_1 = 6.77$, $P < 0.001$).

We related the proportion of females that replaced or did not replace clutches to the date of clutch loss. Most relaying females incurred the loss of their clutch before the 15th day of the incubation. The majority of females that refrained from laying replacement clutches lost their first clutch after the 15th day of incubation (Lapwing χ^2_1 = 4.80, $P < 0.05$; Black-tailed Godwit χ^2_1 = 5.22, $P < 0.02$). The shortest recorded time interval between losing a first clutch and laying the first egg of a replacement clutch was seven days for Lapwings and eight days for Black-tailed Godwits. The longest recorded time interval was 17 days for Lapwings and 20 days for Black-tailed Godwits. The mean (± SD) for Lapwings was 10.86 ± 2.47 days and for Black-tailed Godwits 12.29 ± 2.55 days; t_1 = 1.14, n.s.). Lapwings that produced replacement clutches before the mean time interval laid eggs with smaller volumes (22.69 ± 0.75 cm^3, n = 5) than Lapwings laying after the mean time interval (24.45 ± 0.84 cm^3, n = 9; difference between categories: t_1 = 4.05, $P < 0.01$). This was also the case with Black-tailed Godwits (earlier than mean: 44.45 ± 0.91 cm^3, n = 8; later than mean: 46.39 ± 0.97 cm^3, n = 6; difference between categories: t_1 = 3.81, $P < 0.01$). There were no significant correlations between replacement interval and female body mass (Lapwing r_{14} = 0.316, n.s.; Black-tailed Godwit r_{14} = 0.205, n.s.). The shortest and greatest distances between first and replacement clutches was 14 m and 94 m for Lapwings, and 27 m and 120 m for Black-tailed Godwits. The differences between the species were significant (means ± SD for Lapwings and Black-tailed Godwits, 56.79 ± 13.77 m, n = 14 and 78.50 ± 20.38 m, n = 14 respectively; Mann-Whitney U-test: z = 2.36, df = 1, P = 0.018).

Multiple regression analysis showed that laying date did not affect clutch survival for either Lapwings or Black-tailed Godwits (Table 2). The body masses of female Lapwings and Black-tailed Godwits that successfully hatched their eggs were higher than for those birds that failed. Egg volumes did not influence clutch survival for either Lapwings or Black-tailed Godwits. In the majority of cases, failure to hatch a clutch was due to nest depredation (63% for Lapwing, and 73% for Black-tailed Godwit).

Chick masses in the first few hours after hatching were recorded for 25 clutches from first nests and six replacements clutches for Lapwings, and 21 first and five replacement clutches for Black-tailed Godwits (combining first and replacement clutches, Lapwings 16.32 ± 1.09 g; Black-tailed Godwits 27.55 ± 1.21 g). In most clutches all four chicks hatched. Exceptions were two eggs from one Lapwing clutch, and three eggs from each of three Lapwing and two Black-tailed Godwit clutches. The duration of incubation for those clutches where chicks were weighed immediately after hatching was 27.76 ± 1.52 days for Lapwings and 28.54 ± 1.30 days for Black-tailed Godwits.

Egg volumes, mass and hatching mass were recorded for 21 first and four replacement Lapwing clutches and for 20 first and three replacement Black-tailed Godwit clutches. In first clutches, there were positive correlations between mean egg volume and mean hatchling mass within a clutch for both species (Lapwings r_{21} = 0.745, P < 0.001; Black-tailed Godwits r_{20} = 0.792, P < 0.001; Fig. 2). In replacement clutches, egg volume and hatchling mass were not significantly correlated, presumably because of the small sample size (Lapwing r_4 = 0.429; Black-tailed Godwit r_3 = 0.655, n.s. in both species). For first and replacement clutches combined, the correlation was significant different from zero (Lapwings r_{25} = 0.843; Black-tailed Godwits r_{23} = 0.901, P < 0.001 in both cases).

Of the females whose chicks were weighed, 25 Lapwings and 21 Black-tailed Godwits tended their chicks during the early tending period (10-15 days after hatching), whereas respectively 7 and 12 of these still tended 25-30 day old chicks. Two Lapwing and two Black-tailed Godwit females tended their chicks hatched from replacement clutches to the age of 10-15 days, but were no longer present when the chicks should have been older. Nineteen Lapwing females and 6 Black-tailed Godwit females guarded 10-15 day old chicks without mates, and 10 Lapwing females and 3 Black-tailed Godwit females guarded their 25-30 day old chicks alone. Brood survival decreased with hatching date for both Lapwings and Black-tailed Godwits (Table 3). Brood survival increased with increasing hatchling mass. Females which tended their chicks together with their mates suffered smaller chick losses failures than lone females.

DISCUSSION

We did not find direct correlations between egg size and hatching success in Lapwings and Black-tailed Godwits. This is perhaps no surprise in view of the fact that predation was the main reason for failures to hatch successfully; it is hard to see how egg size could affect risk of predation. However, as in other species (Ricklefs *et al.* 1978), the size of the chick of both species is closely related to the size of the egg, and the survival value of large eggs is nevertheless higher than the survival value of small eggs. In both Lapwings and Black-tailed Godwits, females laying and hatching large eggs were observed to guard chicks that were almost ready to fledge (25-30 days), but those that produced smaller and lighter eggs were not observed to even guard young chicks, 10-15 days old. We suggest that the higher survival value of chicks hatched from large eggs may be mediated by differences in female body condition affecting both egg size/mass, and the females' effectiveness during chick-rearing.

Some precocial bird species lose mass during the incubation period by a reduction in food intake or by fasting (Lessells *et al.* 1979; Mrosovsky & Sherry 1980; Aldrich & Raveling 1983; Mallory & Weatherhead 1993). Female Lapwings and Black-tailed Godwits lost mass between the early incubation period of the first clutch and the early incubation period of replacement clutch. However, the fact that only heavier females laid replacement clutches suggests that the reproductive capacity of lighter females is lower. In both species egg size and chick mass were smaller in replacement clutches than in first clutches. These differences may reflect aspects of the 'cost of reproduction'.

That chicks hatched early in the season tended to survive better than those hatched later, as has also been found before, e.g. for Oystercatchers *Haematopus ostralegus* (Harris 1969; Heppleston 1972) and for Lapwings (Klomp & Speek 1971; Galbraith 1988). Our observations also confirmed, both for Lapwings and Black-tailed Godwits, that chicks have a higher chance to become independent if they hatch earlier. Some males deserted their families during chick rearing. Females taking care of their precocial chicks alone suffered greater losses than females that received help from their mates. The relatively high incidence of polygamy among bird species with precocial young has been explained by the smaller demand for parental care in these species (Lack 1968; Orians 1969). Our findings suggest that biparental care may often be necessary for the successful rearing of offspring in Lapwing and in Black-tailed Godwits.

ACKNOWLEDGEMENTS

We are indebted to Albert Beintema and Ole Thorup for their constructive comments and suggestions. We are grateful to Susan Totterdell, Department of Pharmacology, University of Oxford for her linguistic corrections. We are indebted to István Hahn, Department of Plant Ecology, Eötvös University, for his help in statistical tests. This work was supported by the Department of General Zoology of Eötvös University, and Hungarian National Foundation for Scientific Research.

REFERENCES

Aldrich T.W. & D.G. Raveling 1983. Effects of experience and body weight on incubation behaviour of Canada Geese. Auk 100: 670-679.

Amundsen T. & J.M. Stokland 1990. Egg size and parental quality influence nestling growth in the Shag. Auk 107: 410-413.

Anderson D.W., H.G. Lumsden & J.J. Hickey 1970. Geographical variation in the eggshells of Common Loons. Can. Field. Nat. 84: 351-356.

Ankney C.D. & A.R. Bisset 1976. An explanation of egg weight variation in the Lesser Snow Goose. J. Wildl. Manage. 40: 729-734.

Batt B.J.D. & H.H. Prince 1978. Some reproductive parameters of Mallard in relation to age, captivity, and geographic origin. J. Wildl. Manage. 42: 834-842.

Beintema A.J. & G.H. Visser 1989. Growth parameters in chicks of Charadriiform birds. Ardea 77: 169-180.

Birkhead T.R. & D.N. Nettleship 1982. The adaptive significance of egg size and laying data in Thick-billed Murres *Uria lomvia*. Ecology 63: 300-306.

Bolton M. 1991. Determinants of chick survival in the Lesser Black-backed Gull: relative contribution of egg size and parental quality. J. Anim. Ecol. 60: 949-960.

Cox D.R. & E.J. Snell 1989. Analysis of binary data. Chapman and Hall, London.

De Steven D. 1978. The influence of age on the breeding biology of the Tree Swallow *Iridoprocne bicolor*. Ibis 120: 516-523.

Furness R.W. 1983. Variations in size and growth of Great Skua *Catharacta skua* chicks in relation to adult age, hatching date, egg volume, brood size and hatching sequence. J. Zool., Lond. 199: 101-116.

Galbraith H. 1988. Effects of egg size and composition on the size, quality and survival of Lapwing *Vanellus vanellus* chicks. J. Zool., Lond. 214: 383-398.

Grant M.C. 1991. Relationship between egg size, chick size at hatching and chick survival in the Whimbrel *Numenius phaeopus*. Ibis 133: 127-133.

Harris M.P. 1969. Effect of laying date on chick production in Oystercatchers and Herring Gulls. Brit. Birds 62: 70-75.

Heppleston P.B. 1972. The comparative breeding ecology of Oystercatchers (*Haematopus ostralegus* L.) in inland and coastal habitats. J. Anim. Ecol. 41: 23-51.

Hoyt D.F. 1979. Practical method for estimating volume and fresh weight of birds eggs. Auk 96: 73-77.

Järvinen A. 1991. Proximate factors affecting egg volume in subarctic hole-nesting passerines. Ornis Fenn. 68: 99-104.

Klomp H. & B.J. Speek 1971. Survival of young Lapwings in relation to time of hatching. Bird Study 18: 229-231.

Labisky R.F. & G.L. Jackson 1969. Production and weight of eggs laid by yearling, 2-, and 3-year-old Pheasants. J. Wildl. Manage. 33: 710-721.

Lack D. 1968. Ecological adaptations for breeding in birds. Methuen, London.

Lessells C.M., R.M. Sibly, M. Owen, & S. Ellis 1979. Weights of female Barnacle Geese during breeding. Wildfowl 30: 72-74.

Lundberg C.A. & R.A. Väisänen 1979. Selective correlation of egg size with chick mortality in the Black-headed Gull *(Larus ridibundus)*. Condor 81: 146-156.

Mallory M.L. & P.J. Weatherhead 1993. Incubation rhythms and mass loss of Common Goldeneyes. Condor 95: 849-859.

Miller E.H. 1979. Egg size in the Least Sandpiper *Calidris minutilla* on Sable Island, Nova Scotia, Canada. Ornis Scand. 10: 10-16.

Moss R.A., A. Watson, P. Rothery & W.W. Glennie 1981. Clutch size, egg size, hatch weight and laying data in relation to early mortality in Red Grouse *Lagopus lagopus scoticus* chicks. Ibis 123: 450-462.

Mrosovsky N. & D.F. Sherry 1980. Animal anorexias. Science 207: 837-842.

Murphy E. C. 1978. Breeding ecology of House Sparrows: spatial variation. Condor 80: 180-193.

Murton R. K., N.J. Westwood & A.J. Isaacson 1974.

Factors affecting egg-weight, body-weight and moult of the Woodpigeon *Columba palumbus*. Ibis 116: 52-73.
Myrberget S. 1977. Size and shape of eggs of Willow Grouse *Lagopus lagopus*. Ornis Scand. 8: 39-46.
Nice M.M. 1937. Studies in the life history of the Song Sparrow. I. Trans. Linn. Soc. New York 4: 1-247.
Nisbet I.C.T. 1978. Dependence of fledging success on egg-size, parental performance and egg-composition among Common and Roseate Terns, *Sterna hirundo* and *S. dougallii*. Ibis 120: 207-215.
Ojanen M., M. Orell & R.A. Väisänen 1979. Role of heredity in egg size variation in the Great Tit *Parus major* and the Pied Flycatcher *Ficedula hypoleuca*. Ornis Scand. 10: 22-28.
Orians G.H. 1969. On the evolution of mating systems in birds and mammals. Am. Nat. 103: 589-603.
Otto C. 1979. Environmental factors affecting egg weight within and between colonies of Fieldfare *Turdus pilaris*. Ornis Scand. 10: 111-116.
Parsons J. 1970. Relationship between egg-size and post-hatching chick mortality in the Herring Gull *(Larus argentatus)*. Nature 228: 1221-1222.
Paton P.W.C. & L. Pank 1986. A technique to mark incubating birds. J. Field Ornithol. 57: 232-233.
Ricklefs R.E., D.C. Hahn & W.A. Montevecchi 1978. The relationship between egg size and chick size in the Laughing Gull and Japanese Quail. Auk 95: 135-144.
Schifferli L. 1973. The effect of egg weight on subsequent growth of nesting Great Tits *Parus major*. Ibis 115: 549-558.
Williams T.D. 1994. Intraspecific variation in egg size and egg composition in birds: effects on offspring fitness. Biol. Rev. 68: 35-59.

SAMENVATTING

In een gebied met verlaten visvijvers in Hongarije (het Kiskunság nationale park, 50 km ten zuiden van Boedapest), werd tussen 1988 en 1995 het broedsucces gevolgd van individueel gekleurmerkte Kieviten en Grutto's die op weegschalen broedden. Hierbij werd gezocht naar de relaties tussen het gewicht en de grootte van de vrouwtjes en van de gelegde eieren en van de pas uitgekomen kuikens aan de ene kant, het broedsucces en de kans op een tweede legsel (indien het eerste verloren was gegaan) aan de andere kant. Wat het meest in het oog springt bij deze studie van 67 Kieviten en 65 Grutto vrouwtjes, is dat de conclusies voor beide soorten helemaal gelijk zijn. Zo is er bij geen van beide soorten een verband te vinden tussen de gemiddelde eigrootte van een legsel en het lichaamsgewicht van het vrouwtje dat deze eieren gelegd heeft. Niettemin bestonden er positieve relaties tussen lichaamsgewicht van het vrouwtje en het uitkomst-succes. Uitkomst-succes was niet afhankelijk van legdatum. Alleen als vrouwtjes hun eieren in de eerste helft van de broedtijd door predatie verloren, produceerden ze in een deel van de gevallen een tweede legsel. De vrouwtjes die een tweede legsel produceerden, waren kort na de leg van het eerste zwaarder dan zij die daarvan af zagen. Na het produceren van het tweede legsel waren de vrouwtjes lichter dan na de eerste eileg, ondanks dat de eieren die tweede keer kleiner waren dan die van het eerste legsel. Het tweede legsel werd nooit later dan 17 dagen (Kievit) of 20 dagen (Grutto) na het eerste geproduceerd, en het nest met het tweede legsel lag nooit meer dan 94 m (Kievit) of 120 m (Grutto) van het eerste. Bij beide soorten leverden grotere eieren grotere eendagskuikens op. Hoe groter het kuiken bij uitkomst was hoe groter ook de kans op overleving. In de loop van het broedseizoen nam de overleving van kuikens af. Hoewel Kieviten en Grutto's hun jongen niet actief voeren, bleek ook de mate van ouderzorg belangrijk voor de overleving van de kuikens. Jongen die door beide ouders werden begeleid hadden een grotere kans om vliegvlug te worden dan kuikens die alleen door hun moeder werden verzorgd. (TP)

Received 22 March 1997, accepted 20 December 1997
Corresponding editor: Theunis Piersma