Fig. 5. Slope of linear regression of organ wet mass on whole-embryo wet mass in Sooty Tern embryos from unpipped eggs. Intercepts and slopes for regression lines in Table 1. Dotted lines define 95% confidence limits.

tow and Tazawa 1991). Growth in linear dimensions of embryos of Sooty Terns was similar to that in Wedge-tailed Shearwaters in that in no instance did the growth accelerate after pipping had occurred.

The striking feature of the results of the present investigation is how similar embryonic growth is in the Sooty Tern and Wedge-tailed Shearwater. The two species belong to different orders and differ substantially in body size. The shearwater's egg has a relatively longer incubation period (Whittow 1984). However, the two species have a similar sequence of events during pipping of the egg, and it is possible that the pattern of organ growth may be related to events during pipping. The strength of this argument is that pipping is known to have a considerable effect on the growth rates of some organs, but further studies of species with different modes of pipping are needed to substantiate this.

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Egg Formation, Brood Survival, and Cost of Reproduction as Clutch-size-determining Factors in Common Goldeneyes

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Three major explanations to account for clutch-size limitation in precocial birds such as Common Goldeneyes (*Bucephala clangula*) are: (1) food limitation for the laying female; (2) lower duckling survival in large broods; and (3) lower adult survival or reduced future fecundity among females laying large clutches and/or rearing large broods (i.e. the cost of reproduction; reviewed by Winkler and Walters 1983). Be-

TABLE 1. Nesting parameters ($\bar{x} \pm$ SE, with n in parentheses) of different treatment groups, and differences between manipulated groups and control group.

Nesting parameter	Egg-removal group	Differ-ence[a]	Control group	Differ-ence[a]	Egg-addition group
Laying date[b]	11 ± 2 (8)		12 ± 2 (21)		14 ± 2 (14)
Clutch size[c]	11.9 ± 1.5 (8)	*	9.0 ± 0.6 (21)	***	13.7 ± 0.9 (14)
Incubation period (days)	25.4 ± 0.7 (7)		27.8 ± 1.1 (9)		29.6 ± 0.9 (10)
Egg success (%)	94 ± 2 (8)		93 ± 3 (21)		92 ± 2 (14)
Initial brood size	11.1 ± 1.4 (8)		8.4 ± 0.7 (21)	***	12.7 ± 0.9 (14)

[a] *t*-test. *, $P < 0.05$; ***, $P < 0.001$.
[b] 1 = 1 April.
[c] Eggs in nest at completion of laying, including manipulation.

cause many precocial species are able to lay and successfully incubate a replacement clutch, food limitation for the laying female can hardly explain clutch size (Rohwer 1984, 1986, Milonoff 1989, Arnold and Rohwer 1991). The long tradition of "egg pulling" seems to contradict this hypothesis as well. For centuries, for example, Finnish people have hung nest boxes for goldeneyes and, when females began to lay, removed eggs one after another. Often 20 or more eggs were harvested from each nest (see also Andersson and Eriksson 1982). Because parents of most precocial birds do not feed their chicks, the concept of an optimal brood size in these species is more controversial than in altricial species (e.g. Lack 1968, Safriel 1975). Waterfowl brood-size-manipulation experiments have shown no effect on offspring survival (Rohwer 1985, Lessells 1986). The evidence for the cost-of-reproduction hypothesis in precocial birds also is equivocal (Dow and Fredga 1984, 1985, Rohwer 1985, Lessells 1986, 1987, Savard and Eadie 1989).

Clutch or brood manipulations are necessary for proper testing of these hypotheses (see Lessells 1986). If food availability for the laying female is the factor limiting clutch size, then females should not lay additional eggs in response to experimental egg removals, or if they do, then the quality of their eggs should be lower and, hence, the hatchability or survival of their chicks should also be lower. If each female has her own optimal brood size, then the survival of chicks in artificially enlarged broods should be lower. If clutch size is limited by the cost of reproduction, then females that lay extra eggs or care for enlarged broods should have lower survival or reduced future fecundity. In this study, we evaluated the three hypotheses of clutch-size limitation in Common Goldeneyes.

Methods.—The study was conducted on Lake Suontee in central Finland (62°35′N, 27°15′E) in 1988. The Common Goldeneye is abundant in the district and the population breeds mostly in nest boxes. Females were divided into three groups: (A) In the egg-removal group, three eggs were removed from each nest (about one egg per day) at the beginning of laying when there were two to three eggs in the nest. (B) For the egg-addition group, three eggs (from group

A or from abandoned nests) were added as soon as incubation was determined to have begun (based on female attendance or egg temperatures). (C) For controls, clutch size was not manipulated.

At the end of incubation, females were banded and their speculums were dyed individual color combinations using water-resistant felt-tip pens. The colors faded quickly, but were usually recognizable for about one month. Nest success and the number of chicks leaving the nest were determined by visiting each nest shortly after the expected hatch date. The study area was checked for broods about twice a week and the number of chicks in each brood was recorded. In calculating chick survival, only observations during the first 30 days after hatching were included. The period over which mortality was calculated began with nest exodus and lasted until the first observation of the brood. The mortality of individual chicks in the brood between successive observations was calculated according to the following formula:

$$M = 1 - (F/I)^{1/d}, \tag{1}$$

where M is the mortality per day, F is the final number of chicks, I is the initial number of chicks, and d is the number of days since the brood left the nest.

The mortality includes possible brood division and amalgamation. However, the survival of young chicks without a female is probably low and the incidence of brood division or amalgamation is not dependent on treatment group. We were not able with certainty to document total brood loss, but we used the brood-vanishing rate as a coarse index of it. Nest boxes were checked the next year (1989) to identify banded females and record their clutch size.

Results.—Egg removal did not diminish the final clutch size of goldeneye females; in fact, it was on average even larger than in the control group (Table 1; see also Andersson and Eriksson 1982). Thus, females replaced the three eggs that had been removed. The final clutch size of females with enlarged clutches was naturally larger than in the control group, but there was no difference before manipulation (normal clutch size of females with enlarged clutches = 10.7 ± SE of 0.9, $t = 1.634$, $P > 0.05$, $n = 35$).

We observed 35 broods at least once after they left

TABLE 2. Reproductive parameters ($\bar{x} \pm$ SE, with n in parentheses) of broods seen at least once after leaving nest, and differences between manipulated groups and control group.

Reproductive parameter	Egg-removal group	Differ-ence[a]	Control group	Differ-ence[a]	Egg-addition group
Laying date[b]	13 ± 2 (7)		12 ± 2 (15)		15 ± 2 (13)
Nest-exodus date[c]	19 ± 2 (7)		24 ± 2 (15)	*	17 ± 2 (13)
Initial brood size	10.9 ± 1.7 (7)		8.8 ± 0.7 (15)	**	12.9 ± 1.0 (13)
Exposure period (days)	6.2 ± 0.9 (7)		7.2 ± 1.3 (15)		8.7 ± 2.0 (13)
Mortality/day	0.019 ± 0.009 (7)		0.034 ± 0.009 (15)		0.048 ± 0.011 (13)
Mean chick production[d]	8.2 (7)		5.2 (15)		6.2 (13)
Brood-vanishing rate (%)[e]	12.5 (8)		28.6 (21)		7.1 (14)

[a] *t*-test. *, $P < 0.05$; **, $P < 0.01$.
[b] 1 = 1 April.
[c] 1 = 1 May.
[d] Calculated to age of 15 days using mean initial brood size and mortality.
[e] Broods that were never seen after nest exodus.

the nest. These broods were used in the following analysis (Table 2). The initial brood size in the egg-addition group was naturally larger than in the other groups. These chicks also left the nest earlier than the control group. However, the mortality of chicks was not correlated with the date they left the nest ($r = 0.190$, $P > 0.05$, $n = 35$). Mortality rate is probably not constant with chick age, but there were no differences in the exposure period between the groups. Mortality of chicks did not differ significantly between the manipulated groups and the control group, but the variation was great. The brood-vanishing rate was greatest in the control group.

The next year 16 females returned to the study area (Table 3). There were no significant differences in return rates between the groups. When comparing the successive clutch sizes of the same individuals, the treatment did not seem to affect the clutch size of the next year.

Discussion.—The egg-formation hypothesis (Lack 1968) did not explain the clutch size of Common Goldeneyes. Females were able to lay three extra eggs without compromising the hatchability of their eggs, the survival of their chicks, or their own survival.

Results did not support the chick-survival hypoth-

esis either (Safriel 1975). The survival of enlarged broods was not significantly lowered, even though those broods started with about three additional chicks. The mean chick production of the egg-addition group was at least the same as in the control group (Table 2).

There was no measurable cost of reproduction for females that laid extra eggs or cared for enlarged broods; return rates were not lowered and the clutch size in the next year was not diminished. However, significant survival costs may be low and cumulative and, thus, hard to discover (Milonoff 1991). Previous research on goldeneyes has provided mixed evidence for the cost of reproduction (Dow and Fredga 1984, Savard and Eadie 1989), but neither of these studies manipulated clutch or brood sizes.

The examined hypotheses did not reliably explain the clutch size of Common Goldeneyes. However, sample sizes were very small for some analyses and the manipulation was done in only one year. According to counts of the Finnish Game and Fisheries Research Institute, 1988 was a good year for breeding Common Goldeneyes (H. Pöysä pers. comm.). In unfavorable years, enlarged broods may fare worse (Boyce and Perrins 1987).

TABLE 3. Return rates of females belonging to different treatment groups and successive clutch sizes of same individuals.

Treatment group	Females		Clutch size		
	In 1988	Returned in 1989[a]	in 1988 ($\bar{x}$)	in 1989 ($\bar{x}$)	Difference[b] ($\bar{x} \pm$ SE)
Egg-removal group	8	5	11.7[c]	10.7	−1.0 ± 3.1
Control group	21	6	10.7	11.2	0.5 ± 2.3
Egg-addition group	14	5	11.0[d]	14.3	3.3 ± 1.7

[a] Differences between treatment groups tested using Fisher's exact test; ns.
[b] Differences between treatment groups tested using Mann-Whitney *U*-test; ns.
[c] Total number of eggs laid minus 3.
[d] Clutch size before addition of eggs.

If these hypotheses are not valid, then what limits clutch size in goldeneyes? Incubation ability does not seem to be limiting; the hatchability of enlarged clutches was as high as normal-sized clutches (see also Eriksson 1979). Nor can the traditional nest-predation hypothesis explain the clutch size of precocial birds (e.g. Lack 1947, Johnsgard 1973, Perrins 1977; however, see Arnold et al. 1987), but the renesting hypothesis (Milonoff 1989, 1991) does not require predation rates to be as high. When testing different hypotheses, it should be remembered that man now causes rapid changes in the environment. Therefore, circumstances to which adaptations have evolved (e.g. predation rates) may have changed, and adaptation to prevailing circumstances may not yet have taken place.

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