GOLDSTEIN, H., D. EISIKOVITZ, AND Y. YOM-TOV. 1986. Infanticide in the Palestine Sunbird. Condor 88:528–529.

HOFSHI, H., M. GERSANI, AND G. KATZIR. 1987. A case of infanticide among Tristram's Grackles *Onychognathus tristramii.* Ibis 129:389–390.

HOWITZ, J. L. 1986. Brood adoption by a male Black-capped Chickadee. Wilson Bull. 98: 312–313.

KENDEIGH, S. C. 1941. Territorial and mating behavior of the House Wren. Ill. Biol. Monogr. 18:1–120.

MØLLER, A. P. 1988. Infanticidal and anti-infanticidal strategies in the Swallow *Hirundo rustica.* Behav. Ecol. Sociobiol. 22:365–371.

ROBERTSON, R. J. AND B. J. STUTCHBURY. 1988. Experimental evidence for sexually selected infanticide in Tree Swallows. Anim. Behav. 36:749–753.

ROHWER, S. 1986. Selection for adoption versus infanticide by replacement "mates" in birds. Current Ornithology 3:353–395.

L. HENRY KERMOTT, *Dept. of Biology, St. Olaf College, Northfield, Minnesota 55057;* L. SCOTT JOHNSON, *Division of Ecology (Behavioural Ecology Group), Dept. of Biological Sciences, Univ. of Calgary, Calgary, Alberta, T2N, 1N4, Canada;* AND HELEN BRINTON *Bird, Game and Fish Reserve, Box 582, Big Horn, Wyoming 82833; Please address correspondence to LSJ at the Calgary address.* *Received 2 May 1989, accepted 22 Aug. 1989.*

Wilson Bull., 102(2), 1990, pp. 336–338

Determinacy of clutch size in Horned and Pied-billed grebes.—Clutch size of altricial birds generally is presumed to be limited by the ability of parents to provide adequate food for nestlings (Lack 1947, Klomp 1970; but see Nur 1986). Factors determining clutch size in precocial birds are more obscure (Winkler and Walters 1983), but the ability of females to produce eggs is thought to be important for many species, especially those with self-feeding young (e.g., Anseriformes; Lack 1967, Ankney and Afton 1988; but see Rohwer 1988). Many researchers have suggested that egg-production costs might also be important for birds with parentally fed young (e.g., Houston et al. 1983, Alisauskas and Ankney 1985, Hails and Turner 1985). The egg-production hypothesis predicts that observed clutch size is smaller than the most productive brood size due to the inability of females to produce additional eggs. However, some species with parentally fed young produce larger than normal clutches when eggs are removed from their nests during laying (reviewed in Klomp 1970; see also Reid 1987, Beukeboom et al. 1988). Such examples of extended egg laying do not support the egg-production hypothesis (Klomp 1970, Rohwer 1986).

Little research has focused on the factors influencing clutch size in grebes (Podicipediformes). McAllister (1958) removed one freshly laid egg (second-, third-, or fourth-laid) from each of 32 Eared Grebe (*Podiceps nigricollis*) nests. Grebes with removal nests produced an average of 3.97 eggs, versus 3.40 for 106 control nests (t-test, $P < 0.01$). Fugle and Rothstein (1977) removed all freshly laid eggs from two Pied-billed Grebe (*Podilymbus podiceps*) nests that they visited daily, beginning with the second- or third-laid eggs. One grebe produced a super-normal clutch of 13 eggs, and the other grebe laid a "normal" clutch of seven. In the present study, I conducted egg-removal and egg-addition experiments with Horned Grebes (*Podiceps auritus*) and a larger sample of Pied-billed Grebes.

Grebes were studied in 1987 and 1988 on small wetlands located near Minnedosa, Manitoba (50°10′N, 99°47′W). Egg-removal experiments involved the removal of eggs 3–6 (5

TABLE 1

MEAN NUMBER OF EGGS LAID BY HORNED AND PIED-BILLED GREBES IN RESPONSE TO EXPERIMENTAL REMOVAL AND ADDITION OF EGGS

Species:	Treatment		
	Four egg removal	Control	Four egg addition
Horned Grebe	8.60 ± 0.89 (5)[a]	6.45 ± 1.63 (11)	6.00 (1)
Pied-billed Grebe	8.14 ± 0.90 (7)	7.33 ± 1.28 (21)	7.50 ± 0.71 (2)
Combined[b]	8.33 ± 0.89 (12)	7.02 ± 1.42 (32)	7.00 ± 1.00 (3)

[a] $\bar{x}$ ± 1 SD (N).
[b] Weighted means.

nests) or 4–7 (11 nests) on the day of laying (e.g., four total eggs were removed from each nest over a 4-, or occasionally 5-, day period). Egg additions involved adding four fresh eggs to nests on days 3 and 4 of egg laying (two eggs were added each day). Controls were nests found during egg laying which were not manipulated. Clutch size represents the total number of eggs laid by the attendant female (i.e., it includes egg-removals but not egg-additions). Clutch size was recorded after laying had ceased for two consecutive days, provided nests were still being incubated. Clutch size data were analyzed using a two-way ANOVA with species and clutch manipulation as main effects (Horned and Pied-billed grebe data were analyzed together due to low sample sizes). Statistical significance was inferred based on Type III Sums-of-Squares (SAS Institute Inc. 1985).

Mean clutch sizes for control nests were 6.5 for Horned Grebes and 7.3 for Pied-billed Grebes (Table 1); this difference was not significant($P_{(\text{species effect})} = 0.17$), although other studies from this area indicate that Pied-billed Grebes lay slightly larger clutches than do Horned Grebes (Sealy 1978, Ferguson and Sealy 1983). Egg removal had a significant influence on total number of eggs laid ($P_{(\text{treatment effect})} = 0.007$), with removal birds laying, on average, 1.3 more eggs than did controls. This effect did not differ statistically between Horned Grebes and Pied-billed Grebes ($P_{(\text{interaction effect})} = 0.28$), although inspection of the data suggests that Horned Grebes may have been more responsive to removals. Few egg-addition nests were obtained; the three nests which reached incubation stage contained normal numbers of host eggs (Table 1).

Horned and Pied-billed grebes did not meet Cole's (1917) definition of indeterminate layers; they did not suspend laying in response to egg-additions and they did not completely compensate for the four eggs removed during removal experiments. Neither did Horned and Pied-billed grebes meet Cole's definition of determinate layers; removal birds laid significantly more eggs than did control birds. These results, like previous studies (McAllister 1958, Fugle and Rothstein 1977), provide ambiguous evidence for the egg-production hypothesis. Some individuals were clearly capable of producing more eggs than normal, thus egg-formation costs would not appear to be constraining clutch size in these individuals. However, some individuals did not respond to removals by producing additional eggs. This may indicate that they were unable to produce additional eggs, or it may indicate only that birds did not receive the proper stimuli necesary to extend egg laying (Klomp 1970, Winkler and Walters 1983, Rohwer 1986).

Acknowledgments.—I thank P. Joyce, P. Martin, K. Mawhinney, and J. Morton for their help in locating grebe nests. C. Blem provided constructive comments on the manuscript. This experiment was conducted during my Ph.D. research on American Coots (*Fulica americana*) which received financial and logistical support from the University of Western

Ontario, the Natural Science & Engineering Research Council of Canada (through D. Ankney), Delta Waterfowl & Wetlands Research Station, Sigma Xi, and the Frank M. Chapman, John K. Cooper, and Josselyn van Tyne memorial funds. Egg removals were conducted under permit from the Canadian Wildlife Service.

LITERATURE CITED

ALISAUSKAS, R. T. AND C. D. ANKNEY. 1985. Nutrient reserves and the energetics of reproduction in American Coots. Auk 102:133–144.

ANKNEY, C. D. AND A. D. AFTON. 1988. Bioenergetics of breeding Northern Shovelers: diet, nutrient reserves, clutch size, and incubation. Condor 90:459–472.

BEUKEBOOM, L., C. DIJKSTRA, S. DAAN, AND T. MEIJER. 1988. Seasonality of clutch size determination in the Kestrel *Falco tinnunculus*: an experimental approach. Ornis Scand. 19:41–48.

COLE, L. J. 1917. Determinate and indeterminate laying cycles in birds. Anat. Rec. 11: 504–505.

FERGUSON, R. AND S. G. SEALY. 1983. Breeding ecology of the Horned Grebe, *Podiceps auritus,* in southwestern Manitoba, Can. Field-Nat. 97:401–408.

FUGLE, G. N. AND S. I. ROTHSTEIN. 1977. Clutch size determination, egg size, and eggshell thickness in the Pied-billed Grebe. Auk 94:371–373.

HAILS, C. J. AND A. K. TURNER. 1985. The role of fat and protein during breeding in the White-bellied Swiftlet (*Collocalia esculenta*). J. Zool. Lond. 206:469–484.

HOUSTON, D. C., P. J. JONES, AND R. M. SIBLY. 1983. The effect of female body condition on egg laying in Lesser Black-backed Gulls *Larus fuscus.* J. Zool. Lond. 200:509–520.

KLOMP, H. 1970. The determination of clutch size in birds. A review. Ardea 58:1–124.

LACK, D. 1947. The significance of clutch-size. Ibis 89:302–352.

———. 1967. The significance of clutch-size in waterfowl. Wildfowl 18:125–128.

MCALLISTER, N. M. 1958. Courtship, hostile behavior, nest-establishment and egg laying in the Eared Grebe (*Podiceps caspicus*). Auk 75:290–311.

NUR, N. 1986. Is clutch size variation in the Blue Tit (*Parus caeruleus*) adaptive? An experimental study. J. Anim. Ecol. 55:983–999.

REID, W. V. 1987. Constraints on clutch size in the Glaucous-winged Gull. Stud. Avian Biol. 10:8–25.

ROHWER, F. C. 1986. Response to D. C. Duncan. Auk 103:638–639.

———. 1988. Inter- and intraspecific relationships between egg size and clutch size in waterfowl. Auk 105:161–176.

SAS INSTITUTE INC. 1985. SAS user's guide: statistics, version 5 edition. SAS Institute Inc., Cary, North Carolina.

SEALY, S. G. 1978. Clutch size and nest placement of Pied-billed Grebes in Manitoba. Wilson Bull. 90:301–302.

WINKLER, D. W. AND J. R. WALTERS. 1983. The determination of clutch size in precocial birds. Curr. Ornithol. 1:33–68.

TODD W. ARNOLD, *Dept. of Zoology, Univ. of Western Ontario, London, Ontario N6A 5B7, Canada.* *Received 1 August 1989, accepted 5 Oct. 1989.*