BARNARD, C. J. 1980. Flock feeding and time budgets in the house sparrow (*Passer domesticus*). Anim. Behav. 28: 295–309.

BERTRAM, B. C. R. 1980. Vigilance and group sizes in ostriches. Anim. Behav. 28: 278–286.

CARACO, T. 1979a. Time budgeting and group size: a test of theory. Ecology 60: 618–627.

———. 1979b. Time budgeting and group size: a theory. Ecology 60: 611–617.

———. 1980. Stochastic dynamics of avian foraging flocks. Amer. Natur. 115: 262–275.

———, S. MARTINDALE, & H. R. PULLIAM. 1980. Avian flocking in the presence of a predator. Nature 285: 400–401.

FRETWELL, S. D. 1972. Populations in a seasonal environment. Monogr. Pop. Biol. 5: 1–219.

LAZARUS, J. 1979. The early warning function of flocking in birds: an experimental study with captive *Quelea*. Anim. Behav. 17: 855–865.

PULLIAM, H. R. 1973. On the advantages of flocking. J. Theoret. Biol. 38: 419–422.

———. 1976. The principle of optimal behavior and the theory of communities. Pp. 311–332 *in* Perspectives in ethology (P. H. Klopfer and P. G. Bateson, Eds.). New York, Plenum Press.

Forced Copulation in Captive Mallards
I. Fertilization of Eggs

JEFFREY T. BURNS, KIMBERLY M. CHENG, AND FRANK MCKINNEY
Department of Ecology and Behavioral Biology, Bell Museum of Natural History,
University of Minnesota, Minneapolis, Minnesota 55455 USA

Forced copulation (FC) has been reported in a number of avian families but it is especially well known in waterfowl (family Anatidae). Often this behavior has been called "rape" in the bird literature, but we feel that it is best to avoid this controversial term. In contrast to pair copulations, which are typically preceded by characteristic displays by both sexes, FCs are preceded by active pursuit, grasping, and overpowering of the female. Ever since Heinroth (1910, 1911) drew attention to this phenomenon, there has been controversy about its significance, especially in the Mallard (*Anas platyrhynchos*) and other dabbling ducks (tribe Anatini). Geyr von Schweppenberg (1924) thought that it occurs after females start incubating and are no longer available to satisfy the sexual urges of males. Christoleit (1929a,b) believed that females do not really try to escape but rather encourage males to chase them and to compete for copulations, thereby ensuring fertilization by the strongest male. Weidmann (1956) concluded that FC is associated with territoriality and is a mechanism whereby a male discourages other pairs from settling on his breeding area. Bezzel (1959) and Wüst (1960) doubted that it is common enough in wild birds to be of significance, and they attributed its occurrence in parks and zoos to abnormally high densities of birds.

In a key study of wild Pintails (*A. acuta*), Smith (1968) demonstrated that aerial pursuits (including FC attempts) peaked in frequency during the egg-laying period, and he suggested that these copulations could be related to fertilization of eggs. Reports that male urban Mallards make FC attempts on their own mates (Bezzel 1959, Raitasuo 1964) have been confirmed by recent studies, and the occurrence of such imposed pair copulations soon after a female has been subjected to FC strongly suggests that sperm competition is going on [Barrett 1973, Barash 1977 for Mallards; McKinney 1975, McKinney and Stolen in prep., for Green-winged Teal (*A. crecca*)]. The experiment on captive Mallards by Elder and Weller (1954), in which they removed males from their mates and checked the fertility of eggs subsequently laid, had already shown that females can store sperm for up to 10 days. Thus, at least in certain species of
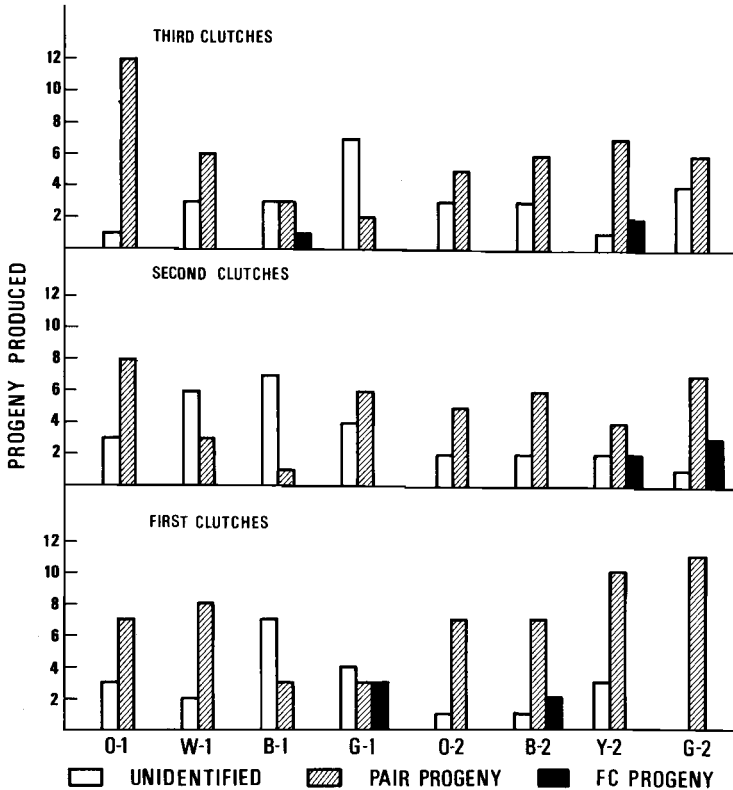
Fig. 1. FC progeny, pair progeny, and unidentified embryos produced by eight captive dusky females.

dabbling duck, FC could be an integral part of the reproductive strategy of paired males (reviewed by McKinney, Derrickson and Mineau, in prep.). Until now, however, there has been no proof that FCs involve actual sperm transfer or subsequent fertilization.

To test whether or not eggs can be fertilized by FC, we used Mallards exhibiting the "dusky" trait. Dusky males lack the white neck ring and chestnut breast of wild-type Mallards, females have a darker than normal plumage, and ducklings are almost entirely black. The dusky trait is recessive (Jaap 1934, Lancaster 1963), so that ducklings from dusky × wild-type matings have the familiar yellow and brown wild-type down pattern. The dusky Mallards used in our study were genetically seven-eighths wild as a result of a 5-yr breeding program involving repeated backcrossing of dusky Mallards from gamefarm stock with wild Mallards at the Northern Prairie Wildlife Research Center, Jamestown, North Dakota (Lee and Nelson 1972). The wild-type Mallards were offspring of birds taken as eggs from nests of wild birds in central North Dakota during the spring of 1976. Because the dusky gene is extremely rare in wild populations, we assume that the wild-type individuals used were homozygous for the dominant wild-type plumage.

In August 1977 we established a flock of 10-week-old Mallards comprised of 16 males (8 wild-type, 8 dusky) and 11 females (all dusky), each marked with a numbered nasal saddle (Sugden and Poston 1968). During the winter they were allowed free choice of mates and were examined weekly for signs of pairing. On 16 April 1978 eight firmly bonded pairs were selected. Two wild-type male + dusky female (WM + DF) pairs and two dusky male + dusky female (DM + DF) pairs were introduced into each of two adjacent flight pens. DM + DF pairs are expected to produce only dusky young, and WM + DF pairs should produce only wild-type young. The appearance of both types of young in a single clutch indicates mixed parentage, barring mutation and the possible occurrence of heterozygous wild-type males in our study flock. With this experimental design we could expect to detect, on average, two out of every three
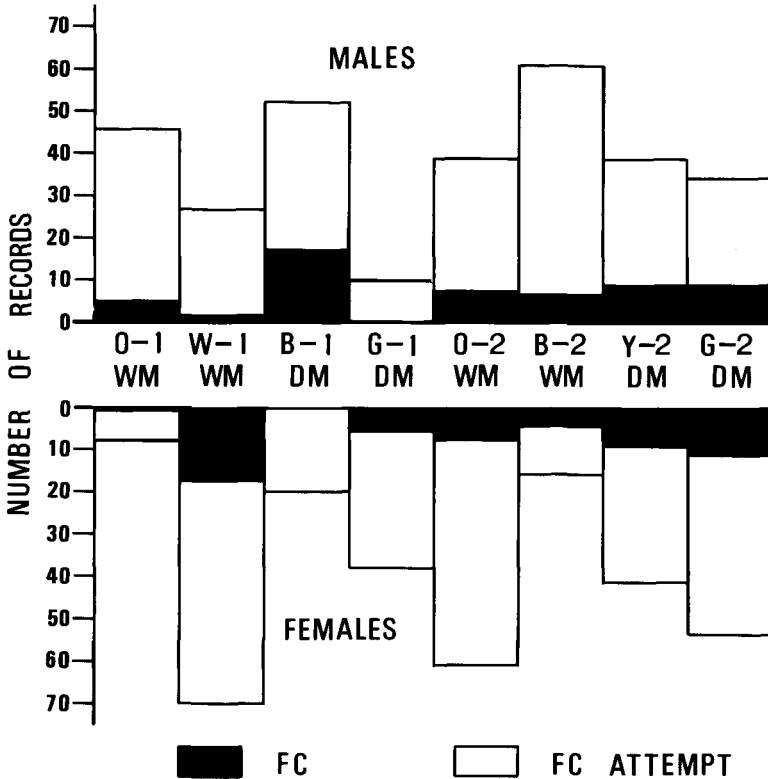
Fig. 2.   Individual involvement of wild-type males (WM), dusky males (DM), and females (all dusky) in FC and FC attempts.

ducklings resulting from FC (i.e. those cases in which the father was of the alternate type to the female's mate).

The flight pens (McKinney 1967) each measured 27.5 m × 27.5 m × 3.6 m, giving enough room for all pairs to establish small territories. Nest scrapes were made by the birds in long grass around the edges of the pens, and by watching them go to their nests we determined which females laid which eggs. Eggs were collected every second day, labelled, and replaced with dummy eggs. When clutches were complete (no new eggs for 2 days), the dummy eggs were removed and the nest destroyed to encourage renesting. We stored the collected eggs in a cool room and incubated them in batches set at about weekly intervals. Eggs were candled on the 7th, 14th, and 21st days of incubation. At the time of the last candling, dead embryos were classified according to phenotype, when possible, and on day 23 all viable eggs were transferred to individual hatching baskets in a "hatcher" incubator. Ducklings were typed 1 or 2 days following hatching.

From 17 April to 21 June we made daily 3-h observations, beginning at sunrise, from a blind over-looking both flight pens. All major interactions (chases, pair copulations, FC attempts) and the nesting activities of each female were recorded. We distinguished "FC attempts" from "FCs" by watching for clues indicating whether the male was successful in achieving intromission. FC attempts entailed pursuit with grasping in the male's bill of some part of the female (nape, back, wing, or tail), and mounting might or might not follow. Our criteria for FC were (1) a pronounced thrust by the male as he bent his tail around the side of the female's tail and (2) a deliberate departure by the male after dismounting, usually with tail-wagging (apparently to retract the "penis"). After dismounting, the male sometimes performed postcopulatory displays (Bridling, Nod-swimming), and sometimes we could see the everted penis, but these were not invariable after FC as judged by our two criteria.

We could identify to type 156 of the 229 eggs laid by the 8 females (3 clutches each). Thirteen (8%) of the identified progeny differed from the expected type (Fig. 1). We observed 58 FCs and 309 FC attempts

(Fig. 2). Females producing 5 of the 13 eggs yielding FC progeny were subjected to FC from males of the appropriate type 1 or 2 days before the laying of the eggs, and FC attempts by males of the appropriate type were seen within 2 days before the laying of 2 more of these eggs.

We could identify 61 ducklings or embryos from first clutches, 45 from second, and 50 from third clutches. Of these, 8%, 11%, and 6%, respectively, were FC progeny, suggesting no seasonal trend. Nor did there appear to be a trend in relation to the sequence of eggs within a clutch.

Although the number of progeny from females paired to dusky males (117 eggs, 74 young) and the number from females paired to wild-type males (112 eggs, 82 young) were nearly equal, wild-type males produced most of the FC progeny (11 of 13, $\chi^2 = 6.63$, $P < 0.05$). We cannot account for this asymmetry, and in fact there were more records of FC by dusky males on the mates of wild-type males (26) than of the reverse (19). Dusky males had a slightly higher success rate in FC attempts than did wild-type males (25% and 19% of contacts leading to FC, respectively). More FCs were recorded in pen 2 (45) than pen 1 (26), and 9 of the 13 FC progeny were produced by pen 2 birds.

In theory, the production of mixed broods by the females we studied could be explained by (1) mutation, (2) the presence of heterozygous wild-type males in our experimental population, (3) females laying in other females' nests, (4) mate-switches, and (5) fertilizations by FC. We discount the possibility of mutations, as the rate required would be unrealistically high. All of the females paired to wild-type males produced at least one clutch comprised only of wild-type ducklings (of those identifiable), suggesting that all of our wild-type males were homozygous. In our daily watches we saw no females laying in other birds' nests, and all clutches were consistent in the distinctive characteristics of the eggs they contained (size, shape, and color of eggs varying between individual females). No mate-switches occurred during the season, and, although females were repeatedly observed copulating with their own mates, they were never observed to solicit copulations from males other than their mate. We conclude that these experiments have demonstrated that FC involves successful intromission and insemination and that this insemination can result in sperm competition and subsequent fertilization of eggs.

These findings must be interpreted cautiously. It seems likely that our captive females were subjected to more FC attempts than would be wild free-ranging birds. The frequency of FC attempts and the proportion of attempts that result in FC in wild Mallards remains an open question. We emphasize that additional research is needed to determine the significance of this phenomenon under natural conditions.

LITERATURE CITED

BARASH, D. P. 1977. Sociobiology of rape in Mallards (*Anas platyrhynchos*): responses of the mated male. Science 197: 788–789.

BARRETT, J. 1973. Breeding behavior of captive Mallards. Unpublished M.S. thesis, Minneapolis, Minnesota, Univ. Minnesota.

BEZZEL, E. 1959. Beiträge zur Biologie der Geschlecter bei Entenvögeln. Anz. Orn. Ges. Bayern 5: 269–355.

CHRISTOLEIT, E. 1929a. Ueber das Reihen der Enten. Beitr. Fortpfl. Vögel 5: 45–53.

———. 1929b. Nochmals das Reihen der Enten. Beitr. Fortpfl. Vögel 5: 212–216.

ELDER, W. H., & M. W. WELLER. 1954. Duration of fertility in the domestic Mallard hen after isolation from the drake. J. Wildl. Mgmt. 18: 495–502.

GEYR VON SCHWEPPENBERG, H. 1924. Zur Sexualethologie der Stockente. J. Ornithol. 72: 102–108.

HEINROTH, O. 1910. Beobachtungen bei einem Einbürgerungsversuch mit der Brautente (*Lampronessa sponsa* L.). J. Ornithol. 58: 101–156.

———. 1911. Beiträge zur Biologie, namentlich Ethologie und Psychologie der Anatiden. Verh. 5th Intern. Ornithol. Kong., 589–702.

JAAP, R. G. 1934. Alleles of the mallard plumage in ducks. Genetics 19: 310.

LANCASTER, F. M. 1963. The inheritance of plumage color in the common duck. Bibliographica Genetica 19: 317–404.

LEE, F., & H. K. NELSON. 1972. Summary of research projects at the Northern Prairie Wildlife Research Center related to hand-reared ducks. Pp. 91–104 *in* Symposium on the role of hand-reared ducks in waterfowl management. Dundee, Illinois, Max McGraw Wildlife Foundation.

McKinney, F. 1967. Breeding behaviour of captive Shovelers. Wildfowl Trust, 18th Ann. Rept. 108–121.

———. 1975. Evolution of duck displays. Pp. 331–357 *in* Function and evolution in behaviour (G. Baerends, C. Beer, and A. Manning, Eds.). Oxford, Clarendon Press.

Raitasuo, K. 1964. Social behaviour of the mallard, *Anas platyrhynchos,* in the course of the annual cycle. Pap. Game Res., Helsinki, No. 24: 1–72.

Smith, R. I. 1968. The social aspects of reproductive behavior in the Pintail. Auk 85: 381–396.

Sugden, L. G., & H. J. Poston. 1968. A nasal marker for ducks. J. Wildl. Mgmt. 32: 984–986.

Weidmann, U. 1956. Verhaltensstudien an der Stockente (*Anas platyrhynchos* L.). I. Das Aktionssystem. Z. Tierpsychol. 13: 208–271.

Wüst, W. 1960. Das Problem des Reihens der Enten besonders von *Anas strepera.* Proc. 12th Intern. Ornithol. Cong., vol 2: 795–800.

Sexual Development During Winter in Male American Woodcock

Thomas H. Roberts
*Department of Wildlife and Fisheries, Mississippi State University, Drawer LW,
Mississippi State, Mississippi 39762 USA*

Recent studies of American Woodcock (*Philohela minor*) have documented that substantial breeding occurs throughout much of the southeastern United States, an area formerly considered to be significant only as a wintering ground (Causey et al. 1974, Stamps and Doerr 1977, Roberts and Dimmick 1978). Woodcock are among the earliest breeders of North American avifauna, but the chronological pattern of their reproductive cycle has not been adequately described. This study was undertaken to delineate the sexual development in the male segment of the population during winter and to determine whether or not physiological differences exist between adult and subadult males.

Woodcock were collected from 17 December 1978 to 26 February 1979. Collection sites were southeastern Louisiana, east-central Mississippi, and western Tennessee. Birds were classified as adults or subadults according to characteristics of the secondaries (Martin 1964). After measurement and fixation in 10% formalin, cross sections of left testes were prepared for histological examination. Sections (6 μ) were stained with hematoxylin and eosine and examined with a binocular microscope under 100×. Based on the degree of gonadal development, males were classified into three groups: Class I—sexually mature (spermatozoa present in all seminiferous tubules); Class II—spermatogenesis occurring but not yet sexually mature (spermatids present in most tubules; spermatozoa present in some cases but only in a few tubules and not in large numbers when present); and Class III—quiescent (only spermatogonia present; no evidence of spermatogenesis).

Forty-seven males were collected during the study. The size of the 43 testes measured ranged from 3.0 mm to 12.0 mm. Considerable variation existed among individuals on any given date, but there was a trend toward increasing testis length during the study period (Fig. 1). There was no significant difference in the regression equations ($P = 0.95$) of adults and subadults when evaluated separately. The earliest date that spermatogenesis was observed was 19 January, while the earliest individual in Class I was collected on 22 January. All birds taken after 1 February ($n = 22$) were in Class I or Class II; 76% were in Class I. The Mann-Whitney u-test (Conover 1971) showed no difference in testis size between 14 adult and 14 subadult males collected during February ($P > 0.1$). Of the subadults shot in February and examined histologically, 91% were in Class I. No difference in either testis size or degree of development that might be attributable to collection site was apparent in the data.

Of 39 testes that were examined histologically, 97% of those greater than or equal to 6.0 mm were in Class I or Class II, with 76% being in Class I. Only 14% of those less than 6.0 mm ($n = 7$) were in Class II; none was in Class I. All less than 5.0 mm ($n = 5$) were in Class III.

Although there was individual variation, the majority of the male woodcock in my sample had attained full breeding condition by early February. Recrudescence of gonads began at least as early as mid-January, although the small number of samples before that period precluded a more precise determi-