CLOACAL PROTUBERANCE AND COPULATORY BEHAVIOR OF THE ALPINE ACCENTOR (*PRUNELLA COLLARIS*)

MASAHIKO NAKAMURA[1]

Laboratory of Animal Ecology, Joetsu University of Education, 1 Yamayashiki, Joetsu City, Niigata 943, Japan

ABSTRACT.—I studied the cloacal protuberance and copulatory behavior of the Alpine Accentor (*Prunella collaris*) over three breeding seasons in central Japan. In males, the seasonal hypertrophy of the glomus seminales forced the posterior wall of the cloaca to form a bulbous cloacal protuberance (16 mm maximum observed diameter) in which sperm were stored. The female's cloaca also protruded from its original position to form a cylindrical protuberance. Its cloacal lips swelled and turned scarlet. The female's protuberance remained swollen for an average of 29.3 days, until the last egg in the first clutch was laid. During renesting or the second breeding attempt, female swelling lasted only 9.4 days. The development period of the male's protuberance was thoroughly overlapped with that of the female. Almost all (98.2% of 431) mating encounters began when the female moved toward the male. In a typical precopulatory sequence, the female exposed the scarlet protuberance toward each of several males in succession, thereby soliciting mountings. Such multiple matings continued throughout the duration of her cloacal swelling. Males performed no sexual displays before they mounted. Each male mated with several females, often in fairly rapid succession, even during the female's presumed *fertile period* (defined as the 9 days before the laying of her clutch's final egg). The unique external sex organs of Alpine Accentors seem to function in their mating system. *Received 7 April 1989, accepted 17 October 1989.*

SPERM competition, where gametes supplied by different males compete for the fertilization of eggs within a single female, is an intense form of postcopulatory male-male competition (Parker 1970). Recent studies of extrapair copulations and multiple paternity in birds (see Fujioka and Yamagishi 1981, Ford 1983, Mock 1983, McKinney et al. 1984, Birkhead et al. 1987 for reviews) indicate that sperm competition may have been an important factor in the evolution of such reproductive behavior as mate guarding and frequent copulation.

Some animal groups, especially insects, show a remarkable range of both reproductive behavior and external sex organs associated with sperm competition (review in Smith 1984, Eberhard 1985). In birds, the ecological significance of the cloacal region has received little attention, because the avian cloaca is actually quite invariant and inconspicuous compared with other morphological features. Among species with severe sperm competition, we can predict that both reproductive behavior and the external sex organs of both sexes may evolve special features.

In most (if not all) passerine males, the seasonal hypertrophy of the *glomus seminales* (seminal vesicles) forces the posterior wall of the cloaca to form a nodular cloacal protuberance (Salt 1954, Wolfson 1954a). It can be used as an external indicator of reproductive capability (Salt 1954, Wolfson 1954a). In contrast, little is known about the female protuberance, and the cloacal region is slightly elevated from the body wall during the breeding season (Wolfson 1954a). Therefore, the cloacal protuberances have often been used to sex various species of Passeriformes (Drost 1938, Mason 1938, McCabe 1943, Wolfson 1952). Although the function of the female protuberance remains unknown, the structure in the male is a site for the storage and maturation of sperm (Salt 1954; Wolfson 1954a, b; Lake 1981). Whether the protuberances are functionally important is still unsolved.

Because the Alpine Accentor (*Prunella collaris*) lacks other sexually dimorphic traits, the external characteristics of the cloacal protuberance are useful for sexing. The male's cloacal region swells considerably to form a definite bulbous

[1] Present address: Laboratory of Animal Sociology, Department of Biology, Faculty of Science, Osaka City University, Sugimoto, Sumiyoshi-ku, Osaka 558, Japan.

protuberance during the breeding season (Fatio 1864, Aichhorn 1969). Wolfson (1954a) reported that the largest reported protuberance is in the Alpine Accentor. The female's cloacal region protrudes and turns scarlet (Aichhorn 1969). The female often exposes the protuberance toward males when she solicits copulation (Aichhorn 1969). These descriptions, however, are fragmentary and no detailed investigation on the protuberance and copulatory behavior has been undertaken.

I studied the changes in the size and characteristics of the cloacal protuberance in relation to the breeding chronology of males and females, the copulatory behavior, and mating system of the Alpine Accentor. I discuss the possible behavioral and ecological functions of the cloacal protuberance.

Materials and Methods

This study was conducted from May through September in 1985–1987 on the 300-ha summit of Mt. Norikura, central Honshu, Japan (Latitude 36°06'N, Longitude 137°33'E). The area's altitude ranges from 2,600 to 3,026 m above sea level; and the summit consists mostly of rocky slopes, alpine meadows, and rocky deserts sparsely populated by dwarf pines (*Pinus pumila*).

The Alpine Accentor is common in the Japanese alpine zone (above 2,600 m) from early May to the end of September. During the breeding season, most individual females make two nesting attempts. Females build their own nests and perform all incubation. The summer social unit is territorial and consists of approximately seven members (mean [$\bar{x}$]: 3.9 males, 3.1 females, n = 22 groups). Each year the site contained nine groups (Nakamura unpubl. data).

To capture the birds and facilitate observation of copulatory behavior, I established one or two artificial feeding grounds (millet seeds in a 30 × 20 cm area) per group. Accentors quickly came to eat, and were captured with a clap net and color-banded. I measured tarsus length, wing length, and body mass. Three cloacal dimensions (see Figs. 1a and 4a) were measured with vernier calipers in each sex. Forty-six males and 41 females were measured a total of 76 and 73 times, respectively. Because the cloacal lip of the female's full-sized protuberance was scarlet and conspicuous, it could be seen easily with binoculars during defecation. I monitored the development of the protuberance among 21 females without capturing them. Captures and recaptures were carried out for 24 days in 1985 (26 June to 5 September), 11 days in 1986 (26 May to 1 September), and 26 days in 1987 (20 May to 25 August).

Body size is a good indicator of age in this species (Nakamura unpubl. data). According to age, the individuals in the study area were divided into two classes: adults (≥2 yr) and subadults. Yearlings or individuals regarded as yearlings from their body sizes were called "subadults."

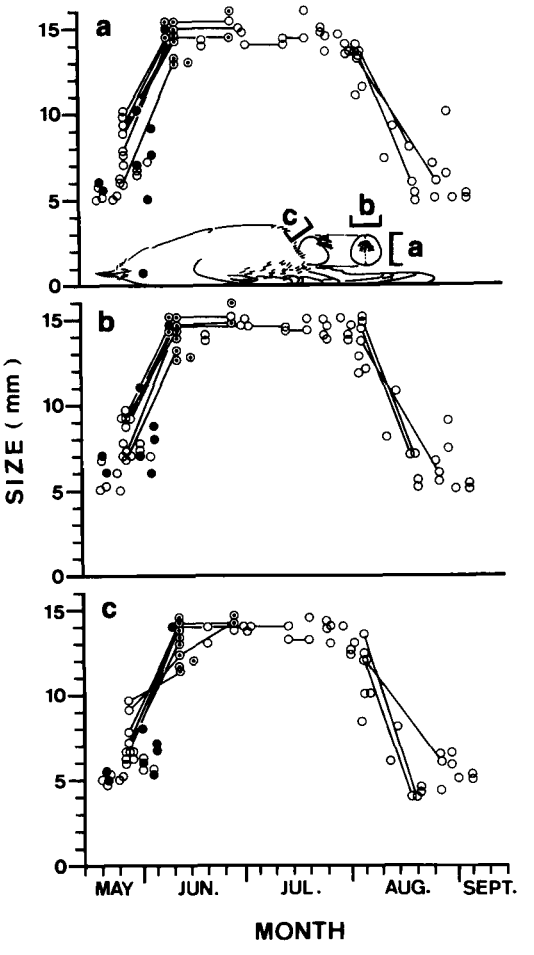

Fig. 1. Seasonal changes in the size of the male protuberance throughout the breeding season (a, b, and c show the seasonal changes in the size of the three labeled dimensions of the cloacal region). Data (n = 76) were pooled for the 3 years. Solid lines connect the data points of the same individual. Solid circles = individuals with pink cloacal lips; open circles with a dot = individuals with glomus seminales visible through the skin.

Detailed observations of copulation were made at two adjacent groups (A and B) in 1986 and 1987. Because accentors copulated frequently at the feeding grounds, I provided food on a daily basis for Group A throughout the breeding seasons in 1986 and 1987, and for Group B in 1987. However, in 1986, Group B was provisioned only during banding or recapture

(for cloacal measurement) operations. Accentors are not shy and I observed copulatory behavior at the feeding grounds through binoculars from distances of 5–10 m. An observation session began as soon as I saw members of the group at the feeding grounds and was uninterrupted from the time members left there until I lost sight of them with a spotting scope. Focal observations of females usually lasted 20 min from the start of the session. I observed copulatory behavior for 44 days in 1986 (15 May to 12 August) and 47 days in 1987 (15 May to 15 August), for a 2-yr total of 562.7 h.

Each female's fertile period was calculated as 9 days before laying of her final egg. It is known that avian sperm can remain viable in the oviductal sperm-host glands for 6–72 days, depending on the species (Lake 1975, Birkhead 1987); but, sperm viability declines with increased storage time (Lodge et al. 1971, Howarth 1974). I adopted the shortest possible limit (6 days). The fertile period was assumed to run until the last egg of the clutch was laid. Female accentors lay 1 egg/day and the average clutch size is 2.7 eggs (range: 2–4, $n = 39$). Thus the entire fertile period began 9 days before the laying of the final egg (see Discussion).

RESULTS

CLOACAL PROTUBERANCE

Males.—The region surrounding the cloaca swelled gradually, from the end of May to mid-June, to form a nodular protuberance. By mid-June, the vent had been relocated several mm from its original position (Fig. 1). During this period, the cloacal lips changed temporarily to pink from the normal gray in eight individuals (30.1%, $n = 26$ males, Fig. 1). When the birds were agitated by handling, the pink lips were withdrawn into the vent and became invisible. The unhandled males would also have pink protuberances. In mid-June, the coiled and distended glomus seminales could be seen distinctly through the stretched skin of the cloaca (Figs. 1 and 2a), but the seminales were no longer visible by the end of June as the skin grew.

Because there was no difference between years (1986 and 1987) in the size of protuberances from 28 May to 1 June (Table 1), data for the two years were pooled. During this period, mean size of each part of the protuberance in adult males was significantly larger than that in subadult males (Table 1).

The peak condition of the protuberance was maintained for ca. 50 days, from the middle of June to the beginning of August. In this state, the cloacal protuberance was a spherical appendage that had only a few feathers on its wall but a tuft of feathers surrounded the vent (Fig. 2b). Once developed, the protuberance showed no changes in size and color (Fig. 1). The fully developed protuberance was formed by two large pear-shaped bodies stuffed with the coiled glomus seminales (Fig. 3). When the seminales were squeezed gently, an exudate was obtained. Examination of the exudate through a microscope revealed it to be sperm. Toward the end of August, the protuberance regressed and disappeared (Fig. 1). Although adult males had significantly greater body masses and longer wings than subadult males, after 12 June their protuberances were equal in size (Table 1).

Females.—By late May, the female's cloacal region protruded posteroventrally, displaced the vent from its original position (Fig. 4), and formed a cylindrical-type protuberance. The female structure developed swiftly (within 3–6 days [$\bar{x} = 5.2 \pm 1.3$ days, $n = 5$ females]), much more rapidly than in males. Of 13 females, 8 (61.5%) showed temporarily pink coloration on the cloacal lips (Fig. 4).

At full size, the female's protuberance appeared as a cylinder, and its cloacal lips turned scarlet (Fig. 2c). Once developed, the protuberance showed no changes in size and color (Fig. 4). The female's cloaca did not exhibit a nodular protuberance as in the male, but it was elevated from the body wall and enlarged. The proctodeum and its thickened outer lips were easily distended and retracted to expose the urodeum and opening of the oviduct when the birds were agitated. Adult females were heavier and had significantly longer wings than subadult females, but protuberance dimensions were similar for the two classes (Table 1).

Development period of female's protuberance.—Once the cloacal protuberance developed, it was

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Fig. 2. Ventral view of cloacal protuberance of males and females: (a) Coiled glomus seminales through the stretched skin of male cloaca; vent (arrow) is surrounded by tuft of feathers; head is upward. (b) Male cloacal protuberance; head to right. (c) Cloacal lips of female protuberance; head is upward.

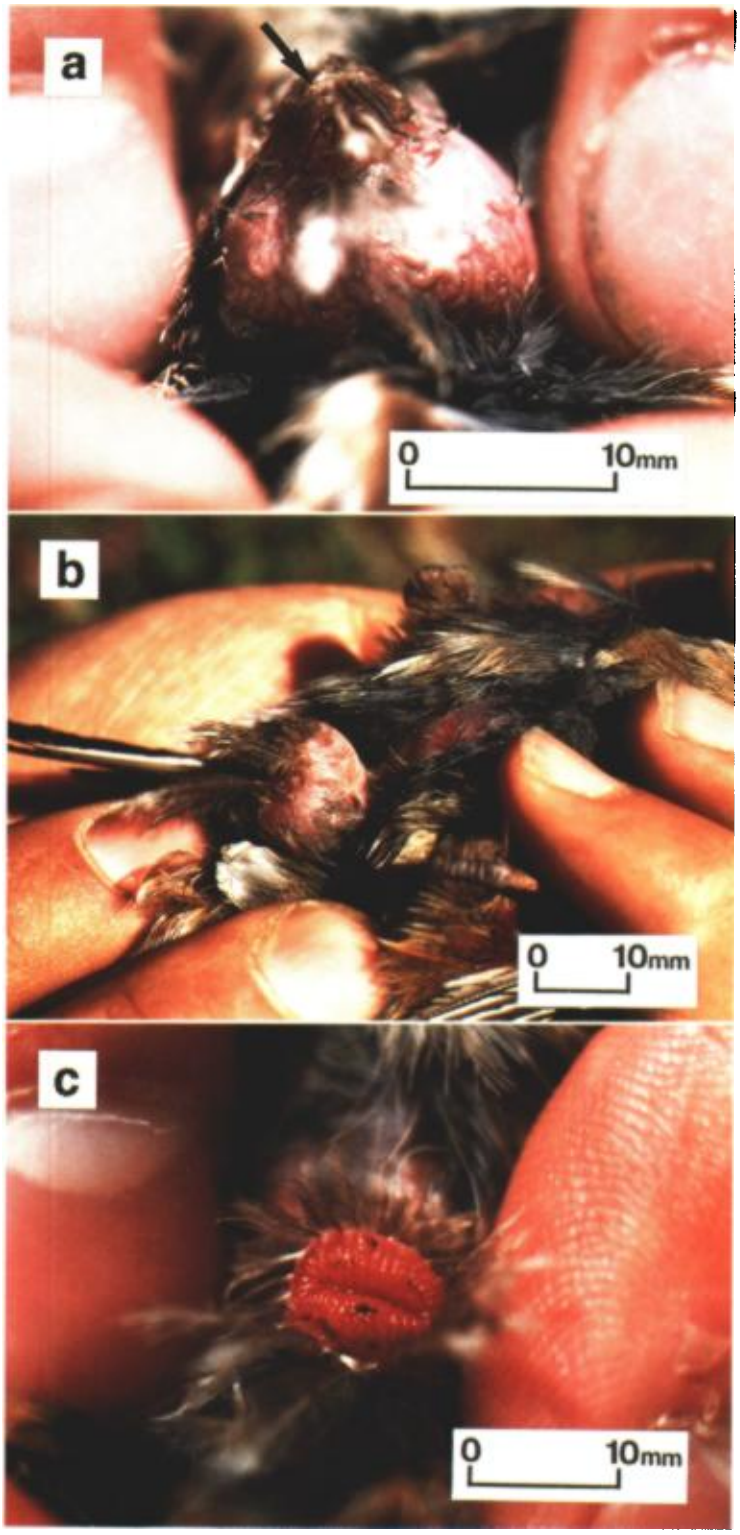
a
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TABLE 1. Body mass, wing length, and protuberance dimensions (all $\bar{x} \pm$ SD) of each sex. Sample sizes are in parentheses. Asterisks[a] indicate significance level for differences between adjacent categories.

	Body mass (g)	Wing length (mm)	Protuberance dimensions[b] (mm)		
			a	b	c
			Male		
28 May–1 June					
1986 (7)	45.51 ± 2.95	105.46 ± 2.77	8.04 ± 1.74	8.24 ± 1.63	7.29 ± 1.37
1987 (7)	44.63 ± 4.57	104.49 ± 2.98	7.49 ± 1.47	8.13 ± 1.04	6.59 ± 1.24
Adult (8)	47.38 ± 1.55 *	106.70 ± 1.96 *	8.74 ± 1.32 *	8.88 ± 1.35 *	7.54 ± 1.38 *
Subadult (7)	42.00 ± 3.59	102.67 ± 2.00	6.47 ± 0.69	7.27 ± 0.40	5.97 ± 0.37
12 June–5 August					
Adult (13)	46.90 ± 1.42 *	106.12 ± 2.00 ***	14.42 ± 0.89	14.18 ± 1.10	12.78 ± 1.77
Subadult (12)	43.34 ± 1.99	100.51 ± 2.35	13.56 ± 1.08	13.89 ± 0.88	12.16 ± 1.59
			Female		
28 May–3 July					
Adult (12)	40.03 ± 2.03 *	98.99 ± 2.14 *	7.23 ± 1.01	8.68 ± 1.23	6.35 ± 0.87
Subadult (10)	36.89 ± 2.85	95.28 ± 2.14	6.86 ± 1.04	7.83 ± 0.60	5.94 ± 0.64

[a] * = $P < 0.05$, *** = $P < 0.01$; two-tailed t-test.

[b] See diagram in Figure 1a (male) and Figure 4a (female).

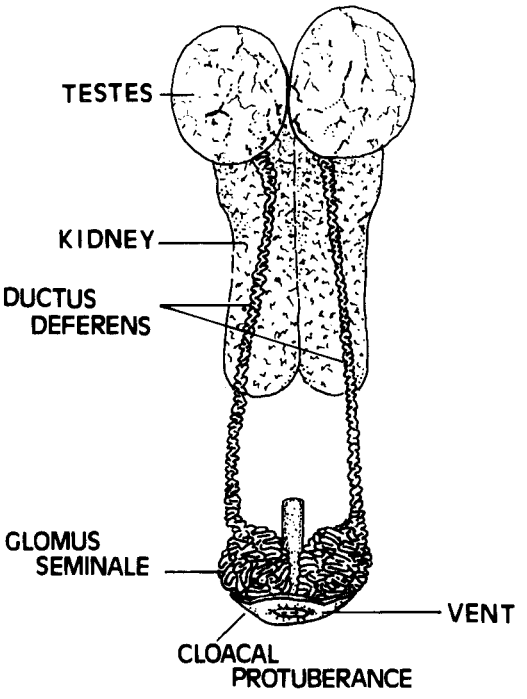

Fig. 3. Diagram of the reproductive organs of a male Alpine Accentor in breeding condition with fully developed cloacal protuberance. Ventral view, diagrammatic, with protuberance pulled posteriorly. Specimen was dissected 23 June 1987 (right testis: 17.6 × 15.1 mm [length × width], 1.5 g [wet mass]; left testis: 19.9 × 17.5 mm, 2.1 g).

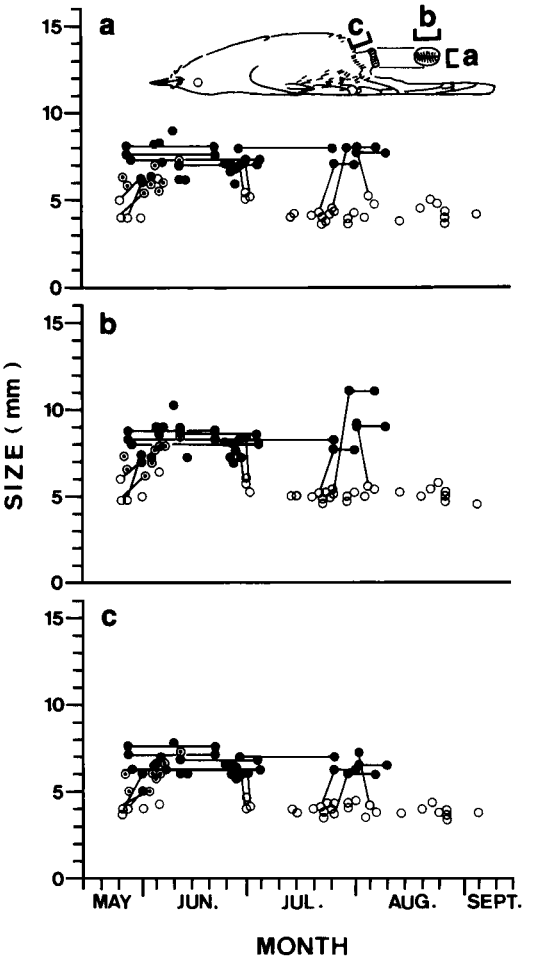

Fig. 4. Seasonal changes in the size of the female protuberance throughout breeding season (a, b, and c show the seasonal changes in the three labeled dimensions). Data (n = 73) were pooled for the 3 years. Solid lines connect the data points of the same individual. Solid circles = individuals whose cloaca formed fully developed protuberance; open circles with a dot = individuals with pink cloacal lips.

maintained until egg laying began. It then regressed and disappeared by the start of incubation (Fig. 5). Incubation began usually the day the last egg was laid (35 of 39 breeding attempts), or it began the day after. Only four females (F2, F87, F9, and F144) had well-developed protuberances for 1–4 days after laying (Fig. 5). There was considerable overlap in the development period of the female's protuberance (Fig. 5).

Because the onset of development showed no difference between years (Table 2), the data were pooled across seasons. Female protuberance development began significantly earlier in adults than in subadults, but the two classes showed no difference in the length of the development period (Table 2). However, development in the first breeding attempt took significantly longer than in the renesting or second breeding attempt (Table 2, U = 0).

Copulatory Behavior

I witnessed 431 mating encounters, including 209 copulations, in 1986 and 1987. Mating encounters were observed throughout the group territory, with higher frequency at the artificial feeding sites (62.0% of all observations). The typical sequence of copulatory behavior was as follows:

(1) Approach: Almost all (98.2% of 431) mating encounters began when the female moved

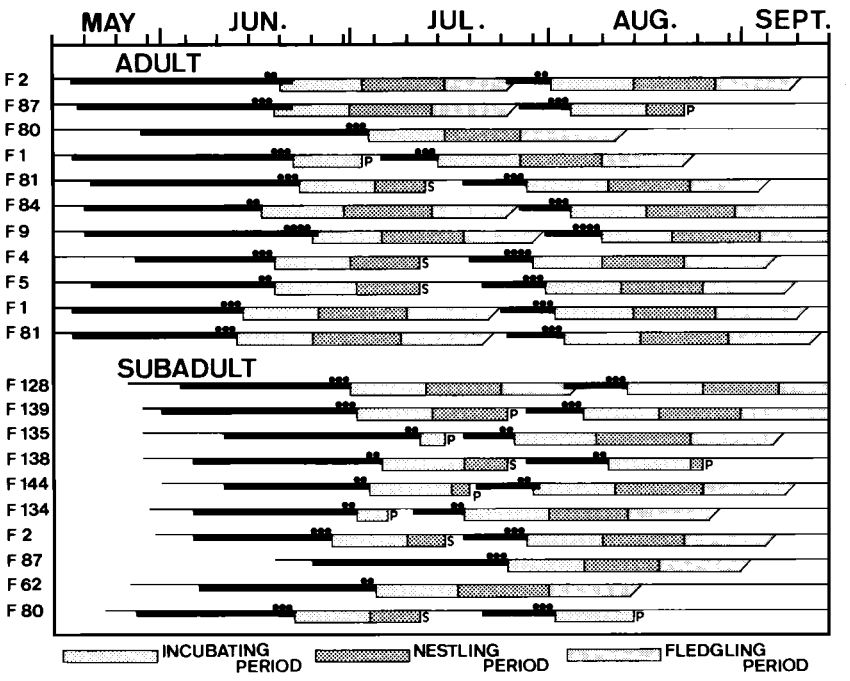

Fig. 5. Seasonal distribution of the development of female protuberance during breeding season. Thick lines = development period of female protuberance; thin lines = residence period; solid circles = egg-laying date; P = nest abandonment owing to predation; S = nest abandonment owing to starvation of nestlings.

toward the male. At such times, the male usually crouched (Fig. 6a). If the male was a long-time group resident, the female began to solicit immediately (Fig. 6d); if he was an unfamiliar male (e.g. subadult), she approached more slowly and stood face-to-face uttering weak calls (Fig. 6b), after which they ran side-by-side for ca. 1 m (Fig. 6c) before the female began to solicit.

(2) Soliciting: The female hopped in front of the male and adopted the "soliciting-posture" (Aichhorn 1969). The female crouched, fluffed her body feathers, shivered her wings, and quivered her steeply raised tail while simultaneously exposing her cloacal protuberance for 2–31 s (n = 50 solicitings, Fig. 6d). One wing was occasionally extended or partly lifted up-

TABLE 2. Comparison of onset and duration ($\bar{x}$ ± SD) of development of female protuberances between adults and subadults. Sample sizes are in parentheses; * = $P < 0.05$ two-tailed Mann-Whitney U-test; NS = $P > 0.05$.

	Adult	Subadult	Mean
Date of first observation[a]			
1986	9.4 ± 3.8 (5)*	25.8 ± 11.7 (4)	16.7 ± 11.5 (9)
1987	6.3 ± 4.3 (6)*	22.3 ± 5.0 (6)	14.3 ± 9.5 (12) NS
$\bar{x}$	7.7 ± 4.2 (11)*	23.7 ± 7.9 (10)	15.3 ± 10.2 (21)
Duration (days)			
First breeding			
1986	29.4 ± 5.7 (5) NS	27.5 ± 3.9 (4)	28.1 ± 4.9 (9)
1987	31.3 ± 4.8 (6) NS	29.2 ± 3.6 (6)	30.3 ± 4.2 (12) NS
$\bar{x}$	30.5 ± 5.1 (11) NS	28.5 ± 3.8 (10)	29.3 ± 4.5 (21)
Renesting and second breeding			
$\bar{x}$	8.9 ± 1.0 (10) NS	10.0 ± 1.5 (8)	9.4 ± 1.3 (18)*

[a] 1 = 15 May.

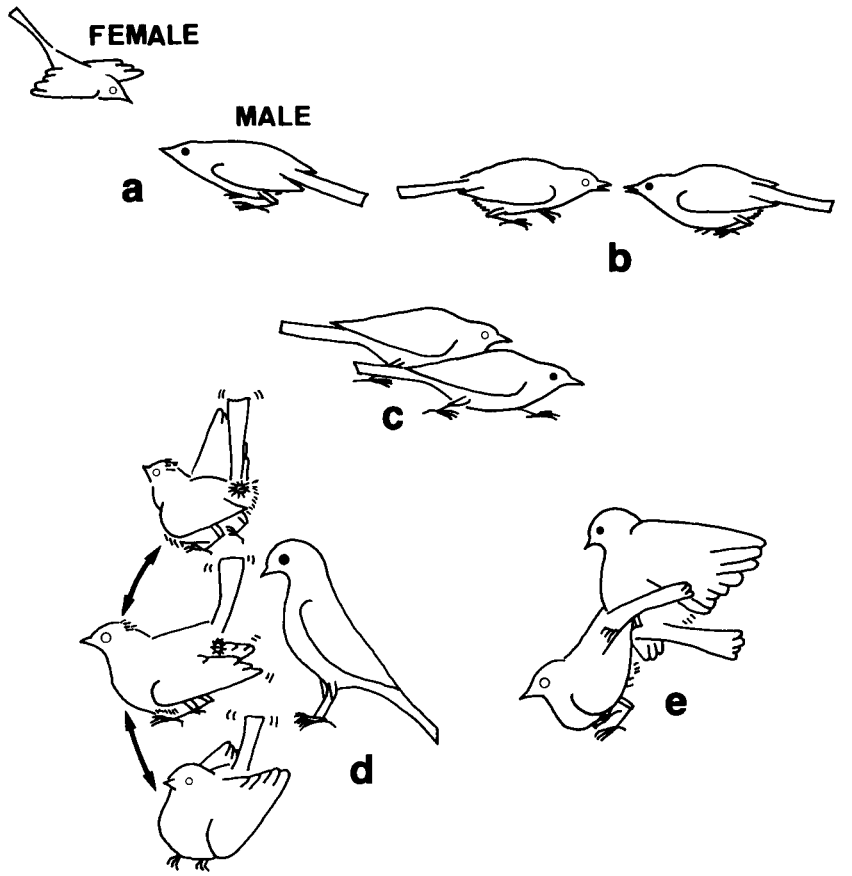

Fig. 6. Main postures and movements related to copulatory behaviors: (a) approach of female to male; (b) confronting; (c) parallel walk; (d) soliciting-postures before copulation; (e) mounting.

ward. The female's cloaca, already scarlet and enlarged, gave strong pumping movements and often (87/381 solicitings) ejected feces. The female repeated soliciting-postures in front of the male, on average 4.1 times per mating encounter (range: 1–22, $n = 431$). This series of events appears to be a courtship display and will be labeled *cloaca-presenting*. In contrast to the female, the male did not perform any sexual displays and seemed only to watch her performance. Cloaca-presenting took place on the ground (81.0% of all observations), on large rocks (10.1%), and on the cottage roofs (8.9%).

(3) Mounting and copulation: The male stood with his legs extended maximally behind the arching female, and briefly looked carefully at her cloacal protuberance. Then the male mounted obliquely from behind the female (Fig. 6e). Copulation was very brief, and the male appeared to jump over the female. As the male pushed off, the female usually fell forward. The female then frequently rushed forward and doubled back so as to position herself once more in front of the male, where she resumed cloaca-presenting. This process was repeated 2–5 times with the same male in rapid succession. The male often sang after copulation. Cloaca-pecking behavior (*sensu* Davies 1983, 1985) was never observed.

(4) Parting: The male usually left the mating site first, either after the female performed cloaca-presenting or after copulation. The female usually followed the male.

Copulation period.—I determined the timing of cloaca-presenting performances for eight breeding cycles with four different females in 1987 (Fig. 7). Cloaca-presenting was observed as soon as the female's cloaca distended to form the protuberance and ceased when it regressed, which was before the start of, or during the

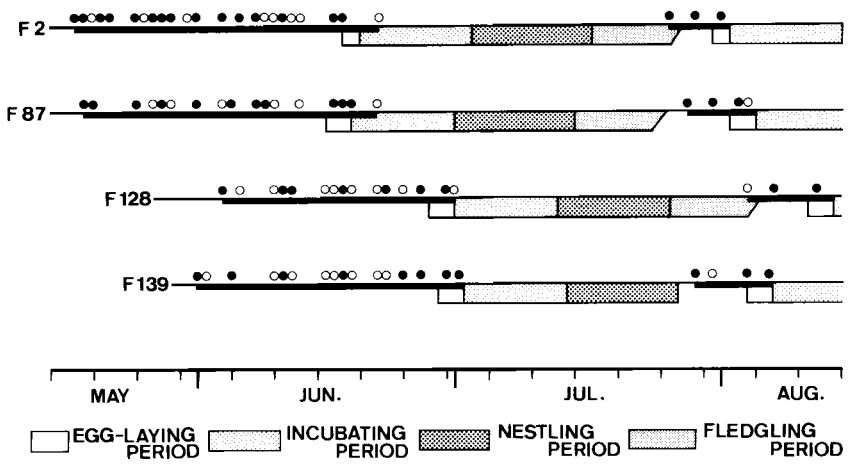

Fig. 7. Development period of female protuberance and days when cloaca-presenting was observed. Thick lines = development period of female protuberance; open symbols = days when the displays were observed; solid symbols = days when copulations were observed.

third day of, incubation (two females: F2 and F87). Males copulated throughout the development period of the female's protuberance (Fig. 7).

SEXUAL RELATIONSHIPS

Within the two intensively studied groups (A and B in 1986 and 1987), all females approached all males. Although the territories of the two groups adjoined and the sexes often met at the border of the territories, females of one group never approached the males of the other group (Fig. 8). Females solicited male group members throughout the protuberance development period and males copulated with them (Fig. 8). Even during the presumed fertile period, all males (excluding two that disappeared) copulated with several females. Females often performed cloaca-presenting toward more than one male in rapid succession. Within Group A, three males copulated with the same female, one after the other in <3 min on 4 June 1987 (Fig. 8).

Because the copulation periods for renesting or second breeding attempts were very short (Table 2) and renestings due to predation occurred suddenly (Fig. 5), all mating encounters were not studied in detail. In these periods, however, more than two males copulated with all females within each group (Fig. 8).

Copulation frequency.—Female approaches to males always led to cloaca-presenting during the copulation period. In Group A, each female approached multiple males on average 0.52 ± 0.30 (SD) times and copulated 0.29 ± 0.18 times per hour in 1986; and in 1987 she approached them 0.95 ± 0.18 times and copulated 0.36 ± 0.16 times per hour. In Group B, each female approached the males on average 0.75 ± 0.45 times and copulated 0.30 ± 0.28 times per hour in 1986; and in 1987 she approached them 0.47 ± 0.28 times and copulated 0.26 ± 0.25 times per hour. The mean hourly rate for females was 0.68 ± 0.34 approaches and 0.30 ± 0.20 attempted copulations. Maximum number of copulations for a female was 32 per day.

DISCUSSION

Within, but not between, groups each female performed cloaca-presenting toward all males in succession, and she copulated with them frequently (Fig. 8). Moreover, the copulation period of each female overlapped considerably and almost all males copulated with females even in the shortest presumed fertile period (Figs. 5 and 8). Therefore, the sexual relationships among the members of a group are multiple matings. Although Group B was not provided an artificial feeding ground in 1986, each female copulated with all male members (Fig. 8). The multiple matings are not caused by extra food. I believe that the inseminations of different males overlapped considerably and their sperm may compete to fertilize an ovum.

The protuberance of female accentors is clas-

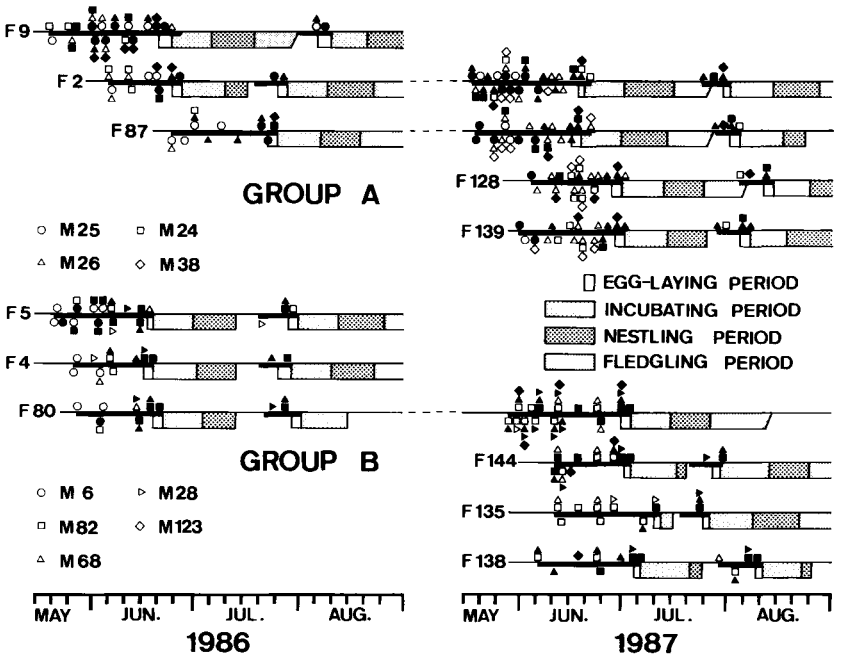

Fig. 8. Sexual relationships within groups A and B in 1986 and 1987. Thick lines = development period of female protuberance; open symbols = days and males that the displays were observed more than one time; solid symbols = days and males that copulations were observed. M25 died on 7 June 1987; M6 died on 5 June 1986; M123 first arrived in 1987.

sified as a cylindrical type (*sensu* Salt 1954, Wolfson 1954a). Female accentors initiated all copulatory events. Males exhibited no obvious precopulatory behavior. Although the male's protuberance may facilitate cloacal contact during copulation (Wolfson 1954b, 1960; Aichhorn 1969), it is difficult to observe actual contact in the field. By contrast, the female cloacal structure seems likely to play an important advertising role during a precopulatory sequence. Only when the cloaca became scarlet and distended did the female display the protuberance toward the males. Similarly, females ceased to perform cloaca-presenting when the structure shrank (Fig. 7). Male accentors never copulated unless females performed cloaca-presenting.

The development period of a female's protuberance corresponded to the copulation period (Fig. 7). The copulation period in the renesting or second breeding attempt ($\bar{x}$ = 9.4 days) was shorter than in the first attempt ($\bar{x}$ = 29.3 days). This means that fertilization of the entire clutch potentially occurs over approximately nine days. This period is almost the same length as the presumed fertile period (see the final paragraph of Materials and Methods). According to these periods, the copulation period in the first breeding attempt may include an extra period for possible fertilization.

The copulatory behavior within groups suggests that females behave actively and may attempt frequent copulations with more than one male. The features of the cloacal protuberance may increase female efficiency. The prolonged development period of the female's protuberance may increase the chance of frequent copulations with several males.

Physiological and anatomical information on female protuberances are generally lacking. In the Dunnock (*Prunella modularis*), the female's cloacal region becomes pink and distended by the cloaca-pecking action of males, which lasts up to 2 min before copulation (Davies 1983, 1985). However, in accentors, I never observed male pecking, and the cloacal region had become scarlet and distended well before the female solicited male attentions. Therefore, enlargement was apparently caused by physiological processes, probably hormonally mediated.

The protuberance of male accentors is a bulbous type (see Salt 1954, Wolfson 1954a). The

male protuberance is formed largely by the growth and coiling of the distal ends of sperm-filled *ductus deferens* (Salt 1954, Wolfson 1954a, Lake 1981). Fatio (1864) estimated that the uncoiled duct of male accentors would be at least 1 m long. Wolfson (1954b) stated that its physiological function is the storage and maturation of sperm, and suggested further that the protuberance may have a thermoregulatory function comparable to that of the mammalian scrotum because the temperature here is several degrees cooler than body temperature.

From the end of May to July, the female's protuberance was intermittently formed according to breeding attempts (Fig. 5). The development period of the male's protuberance overlapped completely with that of the female's (Figs. 1 and 5). I assume that the male structure functions to store sperm, and the male is capable of successful copulations during the breeding season.

Assuming that a female completes approximately four copulations/day (0.30 copulations per hour × 14 h), I estimate the total number of copulations by a female before incubation to be 123 times (4.2 copulations/day × 29.3 days) during the first breeding attempt and to be 39 times (4.2 × 9.4 days) during the renesting or second breeding attempt. These numbers of copulations per clutch are very large compared with other passerine birds (cf. Birkhead et al. 1987, Table 1). Consequently, male accentors produce and store a large volume of sperm for their frequent copulations with several females.

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LITERATURE CITED

AICHHORN, A. 1969. Lautäußerungen des Schneefinken (*Montifringilla nivalis* Linnaeus) und Begattungsverhalten der Alpenbraunelle (*Prunella collaris* Scopoli). Verh. Deutschen Zool. Ges. 32: 690–706.

BIRKHEAD, T. R. 1987. Prolonged sperm storage duration in domesticated canaries. Auk 104: 770–771.

———, L. ATKIN, & A. P. MØLLER. 1987. Copulation behaviour of birds. Behaviour 101: 101–138.

DAVIES, N. B. 1983. Polyandry, cloaca-pecking and sperm competition in Dunnocks. Nature 302: 334–336.

———. 1985. Cooperation and conflict among Dunnocks, *Prunella modularis*, in a variable mating system. Anim. Behav. 33: 628–648.

DROST, R. 1938. Geschlechtsbestimmung lebender Vögel nach der Form der Kloakengegend. Der Vogelzug 9: 102–105.

EBERHARD, W. G. 1985. Sexual selection and animal genitalia. Cambridge, Harvard Univ. Press.

FATIO, M. V. 1864. Note sur une particularité de l'appareil reproducteur mâle chez l'*Accentor alpinus*. Rev. et Mag. de Zool. 27: 65–67.

FORD, N. L. 1983. Variation in mate fidelity in monogamous birds. Pp. 329–356. *in* Current ornithology, vol. 1 (R. F. Johnston, Ed.). New York and London, Plenum Press.

FUJIOKA, M., & S. YAMAGISHI. 1981. Extramarital and pair copulations in the Cattle Egret. Auk 98: 134–144.

HOWARTH, B., JR. 1974. Sperm storage as a function of the female reproductive tract. Pp. 237–270 *in* The oviduct and its functions (A. D. Johnson and C. W. Foley, Eds.). New York, Academic Press.

LAKE, P. E. 1975. Gamete production and the fertile period, with particular reference to domesticated birds. Symp. Zool. Soc. London 35: 225–244.

———. 1981. Male genital organs. Pp. 1–61 *in* Form and function in birds, vol. 2 (A. S. King and J. McLelland, Eds.). London and New York, Academic Press.

LODGE, J. R., N. S. FECHHEIMER, & R. G. JAAP. 1971. The relationship of *in vivo* sperm storage interval to fertility and embryonic survival in the chicken. Biol. Reprod. 5: 252–257.

MASON, E. A. 1938. Determining sex in breeding birds. Bird-Banding 9: 46–48.

MCCABE, T. T. 1943. An aspect of collectors' technique. Auk 60: 550–558.

MCKINNEY, F., K. M. CHENG, & D. J. BRUGGERS. 1984. Sperm competition in apparently monogamous birds. Pp. 523–545 *in* Sperm competition and the evolution of animal mating systems (R. L. Smith, Ed.). New York, Academic Press.

MOCK, D. W. 1983. On the study of avian mating systems. Pp. 1–10 *in* Perspectives in ornithology (A. H. Brush and G. A. Clark, Eds.). Cambridge, Cambridge Univ. Press.

PARKER, G. A. 1970. Sperm competition and its evolutionary consequences in the insects. Biol. Rev. 45: 525–567.

SALT, W. R. 1954. The structure of the cloacal protuberance of the Vesper Sparrow (*Pooecetes gramineus*) and certain other passerine birds. Auk 71: 64–73.

SMITH, R. L. 1984. Sperm competition and the evolution of animal mating systems (R. L. Smith, Ed.). New York, Academic Press.

WOLFSON, A. 1952. The cloacal protuberance—a means for determining breeding condition in live male passerines. Bird-Banding 23: 159–165.

———. 1954a. Notes on the cloacal protuberance, seminal vesicles, and a possible copulatory organ in male passerine birds. Bull. Chicago Acad. Sci. 10: 1–23.

———. 1954b. Sperm storage at lower-than-body temperature outside the body cavity in some passerine birds. Science New York 120: 68–71.

———. 1960. The ejaculate and the nature of coition in some passerine birds. Ibis 102: 124–125.

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100 Years Ago in The Auk

Excerpt from "General Notes" (1890, Auk 7: 203–204):

"**The Great Auk in the U.S. National Museum.**—The Great Auk in the collection of the U.S. National Museum has recently been remounted by Mr. N. R. Wood, and is thereby greatly improved in appearance. Although the specimen is more than fifty years old, the skin proved to be in fair condition, although naturally so venerable a bird needed careful manipulation.

"Like nearly all mounted specimens of the Great Auk this was far too long, and even now that it has been shortened between two and three inches still remains at least so much longer than in life.

"Measured along the curve the length of the stuffed specimen is a little more than twenty-nine inches from tip of beak to root of tail, while a large skeleton, similarly measured, is but a trifle more than twenty-five inches in length.

"A life-sized, colored photograph of the bird as it appeared before remounting is preserved in the collection.—F. A. LUCAS, *Washington, D.C.*"