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SEASONAL PATTERN OF REVERSE MOUNTING IN THE GROOVE-BILLED ANI (*CROTOPHAGA SULCIROSTRIS*)[1]

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Abstract. We observed reverse mounting behavior in a color-banded population of Groove-billed Anis (*Crotophaga sulcirostris*) in Costa Rica. Sex was determined with measurements and laparotomies. Reverse mounting appeared nearly identical to mounting by males. Of 27 mountings in which at least one bird was banded, 15 were reverse mountings. Only reverse mountings (11 observations) were observed in the pre-breeding period. During the breeding season males mounted females in 12 of 16 mountings; one of the reverse mountings followed nest predation. The timing of reverse mounting in anis suggests that it has an adaptive function in courtship. The proximate mechanism may be differential timing between partners in the development of breeding condition or of sexual motivation.

Key words: *Groove-billed Ani;* Crotophaga sulcirostris; *communal breeding; cooperative breeding; copulation; joint nesting; reverse mounting.*

INTRODUCTION

Reverse mounting, in which the female mounts the male, has intrigued ornithologists and behaviorists for many years (Glick 1954; Morris 1954, 1955; Kilham 1958, 1961, 1977; Hauser 1959; Thompson and Lanyon 1979). The proposed explanations for this behavior can be grouped into three classes. The first explains reverse mounting as aberrant behavior, due to a hormonal or structural abnormality (Morris 1954, 1955). Explanations in the second class emphasize the behavioral mechanisms that cause reverse mounting. Examples of such explanations are that the female is dominant to the male (Morris 1954, 1955), that a releasing stimulus is present which elicits male sexual behavior (i.e., the male crouches, which stimulates the female to mount) (Morris 1954, 1955; Ficken 1963; Nolan 1978; Thompson and Lanyon 1979), and that breeding condition or sexual motivation develops asynchronously in the members of a pair (Whitman 1919 cited in Morris 1955; Morris 1954, 1955; Kilham 1961; Stickel 1965; Nolan 1978; Thompson and Lanyon 1979; James 1983; Bowman and Curley 1986). Explanations in the third class emphasize the role of reverse mounting as an adaptive behavior in courtship (Glick 1954, Hauser 1959, Storer 1976, James 1983, Nuechterlein and Storer 1989). Explanations in the second and third classes are not mutually exclusive.

Most of the literature on reverse mounting consists of short descriptions of one or a few episodes, with discussions of the possible reasons for its occurrence. Nuechterlein and Storer (1989) reported the first population study on the occurrence of reverse mounting. They concluded that reverse mounting is an integral part of the courtship behavior of grebes. They found that, in the Silvery Grebe (*Podiceps occipitalis*) and Hooded Grebe (*P. gallardoi*), reverse mounting was more frequent early in the nesting season, at the time of pair formation, than during egg laying. We report here our observations of reverse mounting in a color-banded population of the Groove-billed Ani (*Crotophaga sulcirostris*). The timing of reverse mounting in anis leads us to suggest that it is due to asynchronous development of reproductive condition in the sexes and that it may function to bring the members of a pair into synchrony.

METHODS

We collected information on mounting in the course of a study of the demography and behavior of Groove-billed Anis in Guanacaste Province, Costa Rica (Vehrencamp et al. 1986, Bowen et al. 1989). Groove-billed Anis commonly live in communal groups in which all females in the breeding unit lay their eggs in a single nest (Skutch 1959, Vehrencamp 1978). Breeding units of one to four monogamous pairs defend a common

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TABLE 1. Temporal distribution of mounting by males (M/F, male on female) and mounting by females (F/M) in Groove-billed Anis. We were not in the study area during January and February.

Mounting	Month									
	Mar.	Apr.	May	June	July	Aug.	Sept.	Oct.	Nov.	Dec.
F/M	2	6	3	1	2	0	0	0	1	0
M/F	0	0	0	0	6	3	2	1	0	0

territory. In this part of the species' range, there are distinct wet and dry seasons. Pre-breeding activity began in late March or early April with the onset of spring rains, but laying usually began in early June. We refer to June through December as the breeding season. Renesting was common after a clutch or brood was taken by a predator, and multiple broods were sometimes produced during a single season. During the nonbreeding season, adult members of breeding units generally remained together on or near their breeding territories (Vehrencamp 1978, Bowen et al. 1989). Pair bonds were usually, but not always, maintained between years. Our observations were made from March through December 1979 and 1980. Approximately half the birds in our study area were color-banded. Sex was determined from measurements of weight and bill height; males tend to weigh more and to have higher bills (Vehrencamp 1978). Laparotomies were performed on birds with intermediate measurements. Mountings were observed opportunistically, usually as we drove through the study area. Mountings we observed usually occurred on fence posts or in trees along the road. When we observed mounting or pre-mounting behavior, we noted the color-band combination of each bird, which bird was on top, whether a courtship offering was presented, and what item was offered.

RESULTS

The behavior pattern during reverse mounting was very similar to that seen during mounting by males. A typical mounting began when one bird approached another with an offering. Offerings were green leaves, which are used to line nests, or insects. In mountings by males, males presented insects on five of 12 occasions; in 15 reverse mountings, females presented insects six times and green leaves twice. On 14 occasions the presence or identity of an offering was not determined. The bird with the offering approached with a characteristic posture; the breast was held up and out, and the offering was in the bill. The bird being approached often crouched. As the first bird mounted, the second spread its wings. Then the bird on top fluttered its wings and wagged its tail. After 5–20 sec, the upper bird's tail dipped down and there appeared to be cloacal contact, lasting less than a second. Simultaneously, the lower bird often took the offering. Although females approached with insects prior to reverse mounting, we never confirmed that males took the food items. Females often took food from males, both in mounting and in courtship feeding. Following the mounting, the upper bird dismounted, and the birds frequently preened themselves. We never observed reverse mounting immediately preceding mounting by males. In many species in which reverse mounting has been observed, the behaviors seen in mounting by females are different from those seen in mounting by males (Glick 1954; Morris 1955; Kilham 1958, 1961, 1977; Brackbill 1969; Nolan 1978; Thompson and Lanyon 1979). Because we did not film the mounting sequences, we cannot provide a thorough analysis of the similarities between female and male mounting. Nor could we determine whether insemination occurred in the reverse mountings we observed.

We observed mounting in all months we were in the study area except December, when we spent just a few days observing anis. We observed 27 mountings in which at least one bird was banded. Of the 16 mountings in which both birds were banded, all involved partners of opposite sexes and eight were reverse mountings. Based on this sample of 16, we assume that the partners were of opposite sexes in all 27 mountings, 15 of which were reverse mountings (Table 1).

The most striking difference between reverse mounting and mounting by males was the seasonal distribution of the two types. From March through May, prior to the initiation of egg laying, only reverse mounting was seen. All eight of the March and April mountings occurred at least 30

days before egg laying was known to have occurred in the study area. Three reverse mountings occurred in May, shortly before the initiation of nesting. Because we may not have found the first nest of the season of all breeding units, we could determine in only two cases how much time elapsed between our observations of reverse mounting and the initiation of egg laying by individual females. In one case, laying began approximately 15 days after the mounting; in the other case, it began 30 days later.

During the breeding season, starting in June, males mounted females in 12 of the 16 mountings we saw. One of the four reverse mountings in this period occurred in the incubation stage and another occurred two days after a nest predation, 11 days prior to the laying of eggs in the replacement nest. We did not know the stage of the nesting cycle of the breeding units in the other two cases.

Both types of mounting occurred in simple pairs and in communal groups that contained two to four breeding pairs. Of sixteen mountings in breeding units for which we had independent information about which individuals were paired, only one was outside of a pair bond. In this case, the male mounted the female. The breeding unit in which this occurred contained four adults. The group may have been building a nest, but it is unlikely that the females were laying eggs at the time.

Both types of mountings could occur within a breeding pair. In two pairs we observed a reverse mounting in the pre-breeding period (April and May), then a mounting by the male in the breeding season (July and September, respectively).

Reverse mounting was not restricted to pairs with young or inexperienced males, as has been suggested for other species (Thompson and Lanyon 1979, James 1983). We knew the age class (first breeding season or older) of males involved in seven reverse mountings, and in only one case was the male in his first breeding season. Likewise, reverse mounting is not restricted to the period of initial formation of the pair bond. In at least two cases, reverse mounting occurred after the birds had been paired for one breeding season.

DISCUSSION

Explanations for reverse mounting fall into three classes: aberrant behavior, behavioral mechanisms, and adaptive communication during courtship. The common occurrence of reverse mounting in anis indicates that the behavior is not aberrant. Nuechterlein and Storer (1989), who observed many reverse mountings in grebes, reached the same conclusion.

Some of the mechanisms invoked to explain reverse mounting seem unlikely to apply to anis. Female dominance (Morris 1955, Storer 1976) is unlikely because females tend to be smaller than males (Vehrencamp 1978), although we have insufficient information on dominance to rule out this possibility. Response by females to a stimulus presented by males (Morris 1954, 1955; Ficken 1963; Nolan 1978; Thompson and Lanyon 1979) is unlikely because the behavioral sequence leading to reverse mounting apparently is initiated by the approach of the female with an offering, rather than by crouching by the male.

The mechanism of differential timing in the development of breeding condition or sexual motivation suggests that reverse mounting may be especially likely in nonmigratory species in which breeding is triggered by environmental changes associated with the onset of the breeding season. Females may respond before males to these changes, leading to reverse mounting during the pre-breeding period. In seasonal habitats, anis typically begin breeding activities after the rainy season starts (Marchant 1960, this study). Our frequent observations of reverse mounting prior to the nesting season are consistent with this explanation. Unfortunately, we do not know whether reverse mounting occurred in the early months of the nonbreeding season or whether the behavior was stimulated by spring rains. Reverse mounting also may occur during the breeding season, after the egg-laying period, if sexual motivation is maintained longer in the nesting cycle in females than in males. We observed one reverse mounting in the incubation stage; similar behavior has been observed in the Red-bellied Woodpecker (*Melanerpes carolinus*; Kilham 1961). In species that renest following nest predation, reverse mounting might occur if females are physiologically more prepared to breed than males. Because regression of testes occurs in Groove-billed Ani males during incubation (Vehrencamp 1982), males may not be prepared to breed immediately following nest predation. We observed one reverse mounting after a nest failure. Reverse mounting has been observed in similar circumstances in other species (Nolan 1978, Thompson and Lanyon 1979, James 1983).

The patterns seen in some other species suggest that reverse mounting has been incorporated as an integral part of courtship, and is adaptive. In Starlings (*Sturnus vulgaris*), woodpeckers, and grebes, reverse mounting is common in the period of pair-bond formation and also may occur immediately before mounting by males (Glick 1954; Kilham 1958, 1977; Nuechterlein and Storer 1989). This pattern suggests that females signal their readiness for breeding by engaging in reverse mounting. In grebes Nuechterlein and Storer (1989) found that functional copulatory movements, such as tail thrusting and ejaculation, were less frequent in reverse mountings than in mountings by males. They suggested that this incompleteness could indicate that reverse mounting is a ritualized behavior. They further suggested that reverse mounting may be common in species like the grebes that are monogamous, monochromatic, and engage in mutual or reciprocal displays.

Reverse mounting may have an adaptive function in Groove-billed Anis even though the species does not have reciprocal courtship displays and does not engage in reverse mounting as a precursor to mounting by males. James (1983: 419) suggested an adaptive function for the Northwestern Crow (*Corvus caurinus*) after nest failure: "After failure, a male's interest may wane somewhat. Reverse mounting may be an unambiguous signal to re-stimulate him for a replacement nest, and as such, would have an adaptive function." Like James, we observed reverse mounting after a nest failure. Reverse mounting prior to the breeding season could likewise be a signal by the female of her intent and readiness to breed. The behavior could then serve to stimulate the male and could be adaptive.

Reverse mounting must be the result of some mechanism, regardless of its adaptive value. The mechanism of differential development of breeding condition or sexual motivation is consistent with the hypothesis that reverse mounting is a signal by the female. These two explanations predict much the same temporal distribution of reverse mounting. We conclude that both are probably operating in anis.

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