THE RELATIONSHIP OF GRAZING CATTLE TO FORAGING RATES IN ANIS

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MANY species of birds regularly forage on organisms that have been flushed by a source other than the birds themselves. This source may be nonliving; Stevenson and Meitzen (1946) report White-tailed Hawks (*Buteo albicaudatus*) coming from as far as 10 miles to follow grass fires in Texas. Similarly, raptors often follow trains to feed on animals they flush; see, for example, Kenyon's (1942) work on Pigeon Hawks (*Falco columbarius*). More commonly, the source is living. A large complex of neotropical birds depends for their food upon arthropods flushed by swarms of army ants (Willis, 1967, 1968). Certain old world hornbills, drongos, and leafbirds follow troops of monkeys to obtain the insects they disturb (Chapin, 1939; Stott, 1947). Many of these feeding associations involve large ungulates. The Brown-headed Cowbird (*Molothrus ater*) originally fed in close association with bison; in modern times this association has shifted to cattle. Many species of herons also feed with cattle; probably the best known of these is the Cattle Egret (*Bubulcus ibis*). Finally two tropical American cuckoos, the Groove-billed Ani (*Crotophaga sulcirostris*) and the Smooth-billed Ani (*Crotophaga ani*), regularly forage with domestic cattle wherever cattle have been introduced into their normal range.

Heatwole (1965) showed that Cattle Egrets in Puerto Rico are benefited in both time and energy by their association with cattle. Rand (1953) showed that the association between Groove-billed Anis and cattle in El Salvador was correlated with a greater feeding rate by the anis at any time of year, but the benefit was greater in the dry season than in the wet season. Very little other work has been done to determine the amount of benefit the foraging birds gain by this practice. The present study was conducted from this point of view on both species of ani in Costa Rica during the wet season of 1969. Each species of ani was watched both foraging with cattle and foraging alone to determine whether or not these birds derive any measurable benefit from their association with cattle.

The foraging habits of the two ani species, as described in detail by Bent (1940), are remarkably similar: both regularly forage in small groups of 6 to 10 birds; both are ground feeders; and both are primarily insectivorous, grasshoppers and other orthopterans making up large proportions of the diet of each. Anis of both species, when foraging with grazing cattle, stay very close to the head or front legs of the

animal. When feeding alone, anis of each species generally walk slowly through the vegetation, often stopping and peering intently at a tuft of grass or a leaf. At such times, the neck may be twisted at odd angles, commonly so that one eye is directed upward. Anis are expert at weaving their way among dense grass stems and often disappear for several minutes at a time if the vegetation is more than 4 inches high.

Methods

I studied Groove-billed Anis at Finca Taboga in Guanacaste Province from 9 through 12 July 1969, and Smooth-billed Anis from 5 to 10 August 1969 near Rincon on the Osa Peninsula in Punterenas Province, Costa Rica. In each case I obtained foraging rates for birds feeding with grazing cattle and for those feeding alone. I took no records for birds foraging near cattle that were not grazing. As it was often impossible to see whether or not a bird had been successful at capturing prey, I assumed, as did Rand (1953), that the attempts were 100 per cent successful. Thus the feeding rates are, in effect, pecking rates.

Because neither species of ani behaved in any detectably different way when foraging with horses or mules rather than with cows, the term "cattle" is used here to include all large domestic ungulates.

As short periods of observation might introduce bias, I decided to disregard any period of less than 4 minutes' duration. Because of the need to follow birds for long periods, no data were taken from birds feeding in tall vegetation where they could not be kept in sight for any significant length of time. This meant that data had to be obtained only from heavily-grazed areas. I found an ideal site at Taboga, where a steep hill overlooking a heavily-grazed pasture enabled me to look down into the vegetation and watch the birds more easily. Although the study plot at Rincon was also heavily grazed, it was flat. I found that if I sat on a stool, both the cattle and the anis approached me far more closely than if I were standing; also the stool's height let me follow the birds more easily than I could if I sat on the ground.

Results

In each species, the individuals that followed cattle gained a measurable advantage in foraging efficiency, as determined by their rate of food capture, over the individuals that fed alone (Tables 1 and 2). Indeed, in each species the feeding rate of birds foraging with cattle was approximately twice that of birds feeding alone. These differences in feeding rates are statistically significant at the 0.01 level, as determined by the Student's t-test.

Moreover, both the feeding rates themselves and the advantage gained by following cattle are strikingly similar in the two species studied here.

Discussion

Although this study is based on only a few days' observations for each species, the data do show differences that are statistically significant, and thus can serve as probable indicators of real phenomena. In addi-

TABLE 1
GROOVE-BILLED ANIS: FINCA TABOGA

Time	Birds	Captures (pecks)	Length of time watched (minutes)	Captures per minute	Minutes per capture
A. Anis foraging in the absence of cattle					
07:36–08:03	1	5	27	0.185	5.40
08:08–08:50	1	6	42	0.143	7.00
09:30–09:55	1	3	25	0.120	8.33
14:20–15:05	2	6	45	0.133	7.50
14:20–15:05		6	45	0.133	7.50
15:15–15:31	2	2	16	0.125	8.00
15:15–15:31		2	16	0.125	8.00
15:38–15:45	2	1	7	0.143	7.00
15:38–15:45		1	7	0.143	7.00
15:54–16:04	2	1.5	10	0.150	6.66
15:54–16:04		1.5	10	0.150	6.66
16:08–16:30	1	3	22	0.137	7.33
16:34–17:00	1	4	26	0.154	6.50
Totals	13	42	298		92.88
Average minutes/capture = 92.88/13 = 7.14					
B. Anis foraging in presence of grazing cattle					
07:40–07:55	1	4	15	0.267	3.75
08:10–08:20	1	3	10	0.300	3.33
08:30–09:00	1	9	30	0.300	3.33
10:00–10:15	1	5	15	0.333	3.00
10:16–10:45	1	9	29	0.300	3.33
14:00–14:10	1	3	10	0.300	3.33
14:47–15:01	1	4	14	0.286	3.50
16:00–16:10	1	4	10	0.400	2.50
16:27–16:53	1	6	26	0.230	4.33
16:55–17:25	2	4.5	30	0.150	5.45
16:55–17:25		4.5	30	0.150	5.45
Totals	11	56	220		41.30
Average minutes/capture = 41.30/11 = 3.75					
$t = 9.62^1$ df = 22					

[1] Indicates significance at the 0.01 level.

tion, the data were restricted to birds feeding in short vegetation. Taller vegetation is far more common in the range of either species, and each species regularly follows cattle in this taller vegetation. Yet it seems reasonable to assume that any advantage shown in this study may be extended to include taller vegetation as well.

Rand's (1953) study has already demonstrated that the Groove-billed Ani benefits by foraging in association with cattle. The present study supports his findings for that species, and also indicates that a similar advantage is obtained by the Smooth-billed Ani. The data further indicate that the advantages gained by the two species are very similar;

TABLE 2
SMOOTH-BILLED ANIS: RINCON

Time	Birds	Captures (pecks)	Length of time watched (minutes)	Captures per minute	Minutes per capture
A. Anis foraging in the absence of cattle					
07:40–07:56	1	2	16	0.125	8.00
08:00–08:09	1	1	9	0.111	9.00
08:15–08:32	1	3	17	0.176	5.66
08:45–08:50	1	1	5	0.200	5.00
08:56–09:05	1	2	9	0.222	4.50
09:00–09:12	1	2	12	0.167	6.00
09:12–09:22	1	1	10	0.100	10.00
09:50–10:22	1	4	32	0.125	8.00
10:39–11:01	1	3	32	0.094	10.66
14:15–14:40	1	4	25	0.160	6.25
14:45–15:02	1	2	17	0.117	8.50
Totals	11	25	184		81.57
Average minutes/capture = 81.57/11 = 7.42					
B. Anis foraging in presence of grazing cattle					
07:14–07:31	1	7	16	0.437	2.28
07:36–07:45	1	3	9	0.333	3.00
07:41–07:45	1	3	4	0.750	1.33
07:50–08:02	1	3	12	0.250	4.00
07:50–08:10	1	8	20	0.400	2.50
07:50–08:02	1	4	12	0.333	3.00
07:57–08:05	1	4	8	0.500	2.00
07:57–08:06	1	5	9	0.555	1.80
08:15–08:35	1	5	20	0.250	4.00
08:55–09:01	1	2	6	0.333	3.00
09:02–09:21	1	5	19	0.263	3.80
09:25–09:35	1	3	10	0.300	3.33
09:50–10:29	1	8	39	0.205	4.99
09:55–10:14	1	4	19	0.210	4.75
10:15–10:32	1	5	17	0.294	3.40
13:30–13:42	1	4	12	0.333	3.00
13:44–13:59	1	4	14	0.285	3.50
Totals	17	77	246		53.68
Average minutes/capture = 53.68/17 = 3.16					
$t = 5.64^1$ df = 26					

[1] Indicates significance at the 0.01 level.

each species obtains approximately twice as many food items per unit time when accompanying cattle as when feeding by itself. A great similarity is also seen between the two species in the feeding rates, both with and without cattle. This was a totally unexpected result, and probably further data should be obtained to confirm this similarity.

The association between the anis and cattle is particularly significant in its evolutionary context. Both species presumably evolved in the

new world tropics where no native large grazing ungulates existed. Hence the following behavior shown by each species must have appeared only after the introduction of cattle into the ranges of the two species, i.e., within approximately the last 400 years. Yet the relation between anis and cattle seems to have been relatively stable for at least 100 years: Bent (1940) quotes P. H. Gosse as mentioning in 1847 that Smooth-billed Anis regularly feed with cattle; Bent (1940) also quotes Skutch as saying that in Costa Rica the common name for the Groove-billed Ani is *"garrapatero,"* or tickeater; such a nickname presumably indicates a long association historically.

Both species may have been preadapted for developing such a feeding association. Each species normally feeds in groups; such groups themselves may flush more insects than would the same number of birds feeding individually. Hence individual anis may normally depend on some outside agent (in this case, the other members of the flock) to flush their food. In addition, the very social nature of each species (Davis, 1940) may have served as a sort of preadaptation, because it may have enhanced the spread of the new foraging pattern. Such a rapid spread of new feeding behavior was clearly shown by Hinde and Fisher (1952) for the habit of piercing the covers of milk bottles by several species of titmice in England.

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