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FRUIT DEFENDERS VS. FRUIT THIEVES: WINTER FORAGING BEHAVIOR IN AMERICAN ROBINS

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Abstract.—The behavior of American Robins (*Turdus migratorius*) foraging on fruits of the nonnative European hawthorn (*Crataegus monogyna*) was studied in relation to territory ownership; individuals defending fruit supplies (owners) were compared with conspecifics intruding on defended territories (intruders). On average, owners had longer feeding bouts, ingested more fruits per bout and foraged for fruits more slowly than intruders. During the first minute after arrival at a fruit source, intruders attempted to pick fruits almost three times as fast and ingested twice as many fruits as owners. These results are important because most studies discussing differences in foraging behavior between owners and intruders have been only anecdotal, and because reports of fruit defense are rare.

DEFENSORES DE FRUTAS VS. LADRONES DE FRUTAS: CONDUCTA DE FORRAJEO INVERNAL DE INDIVIDUOS DE *TURDUS MIGRATORIUS*

Sinopsis.—Se estudió la conducta de forrajeo del Petirrojo Americano (*Turdus migratorius*) sobre frutas del exótico *Crataegus monogyna,* en relación a la posesión de territorios. Se compararon individuos que defendían frutas (dueños) en su territorio con individuos que invadían dichos territorios (intrusos). En promedio, los dueños forrajearon más pausadamente, exhibieron periodos mayores de alimentación e ingirieron mayor cantidad de frutas que los intrusos. Durante el primer minuto de haber llegado a una fuente de alimento, los intrusos intentaron ingerir frutas tres veces más rapido e ingirieron el doble de las frutas que los dueños. Estos resultados son importantes porque los estudios que discuten diferencias en conducta de forrajeo entre dueños e intrusos son de carácter anecdótico, y además porque los informes de defensa de recursos alimentarios como frutas son muy raros.

Several studies of birds have addressed the defense of a resource by dominant territory owners against intruding conspecifics. Such studies usually have concerned aggressive defense behavior *per se,* focusing on aggressive interactions between territory owners and different kinds of intruders (e.g., Dulude et al. 1989; Moore 1978; Temeles 1989, 1990). Fewer studies have considered the foraging behavior of territory owners, and especially territorial intruders (e.g., Carpenter et al. 1991, Davies and Houston 1981, Frost and Frost 1980, Paton and Carpenter 1984, Richner 1989).

To examine whether foraging behavior varied between owners and intruders, I studied wintering American Robins, *Turdus migratorius,* feeding on fruits of the nonnative European hawthorn, *Crataegus monogyna.* I compared the behavior of territorial birds ("owners") defending fruiting hawthorn bushes, with that of conspecifics intruding on their territories to feed ("intruders"). Territorial defense of fruits by robins (see also Pietz and Pietz 1987, Young 1956) lasted only a few days during which temperatures remained unusually low (ranging from −15 to 1 C). Resource

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TABLE 1. Summary of differences in foraging behavior between owners and intruders. Values are based upon 24 owner feeding bouts and 10 intruder feeding bouts, and are means ± SD.

	Owners	Intruders
Feeding bout length (min)	7.65 ± 1.22	1.44 ± 0.79
# fruits eaten per bout	13.83 ± 2.35	5.10 ± 2.09
# fruits eaten per min	1.86 ± 0.44	3.87 ± 1.20

defense by frugivorous birds is rare; despite 30 yr of research on frugivory, only a few cases of fruit defense have been observed (e.g., Logan 1987; Moore 1977, 1978; Pietz and Pietz 1987; Pratt 1986; Snow and Snow 1984) or experimentally induced (Tye 1986).

METHODS

I collected data on six birds (three owners and three intruders) over 15 h on three consecutive days (5–7 Feb. 1989). Each owner defended a territory (1–3 bushes) against one intruder and each owner/intruder pair was observed on a different day and at a different location on the Nature Conservancy's Cogswell-Foster Preserve in Linn County, western Oregon. All observations were made between 1300 and 1800 hours (sunset). Although birds were not banded, I was confident I could distinguish individuals using characteristic variations in plumage (e.g., white on tail-feathers, unusually large eye-ring, heavily speckled breast and dark crown) and behavior (e.g., consistent use of the same perch and route in leaving and returning to the territory). Owners regularly left their territories for approximately 2–6 min (mean ± SE = 3.76 ± 0.37 min) to drink melting snow. During these periods owners could be observed at all times and did not eat anything. Intruders arrived while owners were away from their territories and fed until chased away by the returning owners.

The foraging behavior of robins was observed directly and recorded on audio tape. Tapes were later analyzed for: (i) total length of a feeding bout; (ii) the number of fruits eaten per feeding bout; and (iii) feeding rate (number of fruits eaten per minute). I defined a feeding bout as the time between the arrival of a bird in a bush and its departure from the bush.

RESULTS

A total of 24 owner feeding bouts and 10 intruder feeding bouts was recorded during the study. Results are summarized in Table 1. Differences in foraging behavior between owners and intruders were tested with a Model II, two-way ANCOVA (using StatView 512+®). "Bird-type" (i.e., owner or intruder), "bird-pair" (i.e., first, second or third) and bird-type × bird-pair interaction were factors in the model. Each series of feeding bouts was numbered sequentially and included as a covariate, nested for each bird. This was done to take into account the tendency for

TABLE 2. Results of the Model II, two-way ANCOVA used to test differences between the foraging behavior of owners and intruders. Bird-type effects (A), bird-pair effects (B), bird-type × bird-pair interaction effects (C) and bout number in sequence effects (D).

	Variable	*F*	df	*P*
(A)	Feeding bout length	42.00	1,2	<0.025
	# fruits eaten/bout	6.40	1,2	>0.10
	Feeding rate	39.76	1,2	<0.025
(B)	Feeding bout length	0.06	2,2	>0.90
	# fruits eaten/bout	0.26	2,2	>0.70
	Feeding rate	0.76	2,2	>0.60
(C)	Feeding bout length	0.69	2,22	>0.50
	# fruits eaten/bout	2.89	2,22	>0.05
	Feeding rate	0.13	2,22	>0.80
(D)	Feeding bout length	0.35	6,22	>0.90
	# fruits eaten/bout	3.24	6,22	<0.05
	Feeding rate	0.69	6,22	>0.60

some birds to ingest more fruits per bout as dusk approached. Feeding bout length, number of fruits eaten per bout, and feeding rate (number of fruits eaten per min) were the dependent variables.

Feeding bout length and feeding rate differed significantly between owners and intruders, whereas the number of fruits eaten did not, even though owners ingested almost three times as many fruits per bout as intruders (Table 2a). Differences between bird-pairs were not significant (Table 2b). The bird-type × bird-pair interactions also were nonsignificant (Table 2c). Bout number in sequence had no effect on feeding bout length or feeding rate, but did significantly affect the number of fruits eaten per bout (Table 2d).

Using a Model II, two-way ANOVA, I further examined differences in foraging behavior between owners and intruders by tracking feeding activity within feeding bouts. As in the previous analysis, "bird-type," "bird-pair" and bird-type × bird-pair interaction were factors in the model. Intruders attempted to pick fruits much faster than owners during the first minute after arriving at the fruit source ($F = 23.60$, df = 1,2, $P < 0.05$; Fig. 1a). When compared for the efficiency with which fruits were picked from branches and subsequently swallowed, no significant difference was found between owners and intruders during the first minute

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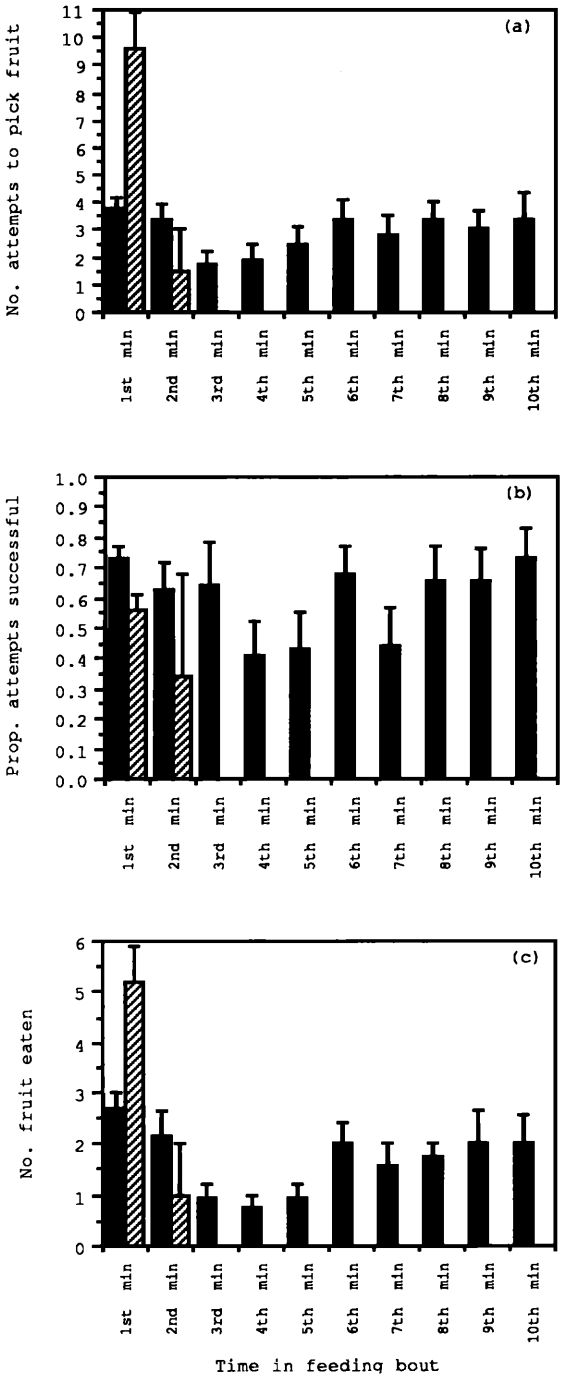
FIGURE 1. (a) Mean (±SE) number of attempts to pick fruit per minute of feeding bout by owners ($n = 24$; solid bars) and intruders ($n = 10$; hatched bars). (b) Mean (±SE) proportion of attempts to pick fruit resulting in fruit acceptance per minute of feeding bout by owners ($n = 24$; solid bars) and intruders ($n = 10$; hatched bars). (c) Mean (±SE) number of fruits eaten per minute of feeding bout by owners ($n = 24$; solid bars) and intruders ($n = 10$; hatched bars).


(a)
No. attempts to pick fruit
0
1
2
3
4
5
6
7
8
9
10
11
1st min
2nd min
3rd min
4th min
5th min
6th min
7th min
8th min
9th min
10th min
(b)
Prop. attempts successful
0.0
0.1
0.2
0.3
0.4
0.5
0.6
0.7
0.8
0.9
1.0
1st min
2nd min
3rd min
4th min
5th min
6th min
7th min
8th min
9th min
10th min
(c)
No. fruit eaten
0
1
2
3
4
5
6
1st min
2nd min
3rd min
4th min
5th min
6th min
7th min
8th min
9th min
10th min
Time in feeding bout

of a feeding bout ($F = 12.75$, df = 1,2, $P > 0.05$; Fig. 1b). Intruders were found to consume significantly more fruits during the first minute of a feeding bout when compared with owners, however ($F = 28.24$, df = 1,2, $P < 0.05$; Fig. 1c).

Figure 1 shows a tremendous drop in the number of attempts to pick fruits, success rate, and the number of fruits eaten by intruders from the first to the second minute of a feeding bout; this drop reflects the fact that returning owners terminated intruder feeding bouts after an average of 1.44 min. In contrast, owner foraging behavior during the first minute of feeding was not significantly different from the rest of the feeding bout (t-test of a single observation [first minute] against a sample mean [entire bout]; number of attempts to pick fruits [Fig. 1a]: $t = 1.37$, df = 8, $P > 0.20$; successfully picking acceptable fruits [Fig. 1b]: $t = 1.08$, df = 8, $P > 0.30$; number of fruits eaten [Fig. 1c]: $t = 1.88$, df = 8, $P > 0.05$). The relatively high feeding activity of intruders during the first minute of a bout therefore probably did not result from some response associated with arrival at a fruit source, or owners would presumably do it too.

DISCUSSION

Why did intruders consume many more fruits during the first minute of a foraging bout compared with owners (Fig. 1c)? Most obviously, intruders must consume fruits rapidly because they are foraging with a major time constraint: the return of and inevitable detection by owners. In contrast, owners might forage slowly because they need to scan for intruders (e.g., Ydenberg 1984, Ydenberg and Krebs 1987) and/or predators (Lima 1991, Lima and Dill 1990 and references therein). When owners were present in their territories, intruders were usually detected before reaching the territory, therefore, vigilance against intruders must have been an important activity for owners. Intruders were clearly less vigilant than owners, and consequently might have been exposing themselves to a higher risk of predation.

Owners and intruders also might differ in their rate of fruit consumption because of different fruit processing schedules. Owners may be limited in the number of fruits they can consume, as well as the rate they can consume them, because, unlike intruders, their digestive tracts are closer to being filled to capacity and they are constrained from consuming more food until some food has cleared the digestive tract (e.g., Levey and Duke 1992, Levey and Grajal 1991). Recent research on the digestive strategies of frugivorous birds has found that the rate of fruit passage through the digestive tract can be "controlled" by the bird (Martínez del Rio and Karasov 1990 and references therein). Essentially, if there are constraints on foraging (such as limited access to food), birds can pass fruits more slowly through the gut to increase the absorption of sugars. Intruders may therefore consume lots of fruits in short bursts (as when intruding upon temporarily vacant territories) and then process them more slowly once they leave territories. In contrast, owners may feed at a more constant

rate and process fruits more rapidly because they are not constrained by access to fruits.

There are some interesting similarities and differences between the frugivore studied here, and the nectarivore studied by Carpenter et al. (1991). Carpenter et al. found feeding bout duration and meal size differences between owner and intruder Anna's Hummingbirds (*Calypte anna*). A general conclusion could be that intruders are very aware of their precarious position and try to "make the most" of their intrusion, perhaps with cost to efficiency.

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If you have such data in your files, would you consider sharing it with the broader wildlife community? Even if you only have laboratory values for one individual of one species, this constitutes valuable information. We are also interested in finding out about any literature on the subject that you might be familiar with. We will compile all available information and make it widely available. For their participation, anyone contributing data will receive full attribution and a copy of the database.

Once our database is a bit more complete we will make it available to veterinarians, wildlife rehabilitators and wildlife biologists by posting it on electronic networks such as Econet, and making available both hard copy and diskette versions at our cost.

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