BEHAVIORAL FLEXIBILITY OF PINE SISKINS IN MIXED SPECIES FORAGING GROUPS

DAVID F. BALPH

AND

MARTHA HATCH BALPH

Davis (1926) observed the behavior of Pine Siskins (*Carduelis pinus*) and Evening Grosbeaks (*Hesperiphona vespertina*) at a winter feeding station provisioned with sunflower seeds. He noted (1926:386-387):

They [the Pine Siskins] were exceedingly fond of sunflower seeds, but their bills were so tender that they were hardly able to crack the hard shells so as to obtain the kernel inside. So they would watch their opportunity, and whenever an Evening Grosbeak came to the feeding-shelf and began cracking the seeds, he would be surrounded by several of the Siskins. As he cracked the seeds, some particles of the kernel would scatter from his beak, and immediately the Siskins would rush in and gobble them up.

In this paper we examine the response described by Davis and changes in the behavior of Pine Siskins as a function of food accessibility.

METHODS

We observed mixed-species foraging groups of Pine Siskins, Evening Grosbeaks, and Cassin's Finches (Carpodacus cassinii) at Logan, Utah during the winter and spring of 1976-77 and 1977-78. From December to April of 1976-77, we provisioned a 0.74 m² elevated platform with Romsun HS-52 sunflower seeds. All three species were able to husk these seeds, which were relatively small (averaging 6 \times 10×4 mm and 0.05 g; n = 10) and soft-shelled. During this period, we did not see Pine Siskins orient toward either of the larger species. By mid-April, our original seed supply was exhausted, and we began to fill the platform with standard confectionary sunflower seeds. Evening Grosbeaks and Cassin's Finches, but not Pine Siskins, were able to husk the new seeds, which were larger (averaging 10 imes 15 imes 6 mm and 0.15 g; n = 10) and harder-shelled than those used earlier. Within a few days, we noticed that Pine Siskins approached and obtained seed particles falling from the bills of Evening Grosbeaks and (to a lesser extent) Cassin's Finches. In some cases a siskin appeared to defend an area beneath a grosbeak's bill against other siskins.

The following winter, when Pine Siskins and Evening Grosbeaks again were present in sizable numbers, we attempted to quantify these responses. We gathered data at the same platform freshly provisioned with sunflower seeds of varying size, observing the birds through one-way glass from a blind. To collect data, we selected a siskin that was within 15 cm of a grosbeak and, during a 5-s period, recorded (1) whether or not the siskin attempted to obtain food particles from the grosbeak and (2) whether or not the grosbeak pecked at the siskin (data type 1). Subsequently, we noted the first agonistic encounter between two siskins occurring within 15 cm of a grosbeak and recorded whether or not the winner approached and attempted to obtain food from the grosbeak within 3 s of the end of the encounter (data type 2). On 24-25 February 1978, we collected 100 samples of each type of data while the two species fed on small (Romsun HS-52) sunflower seeds, which we had supplied ad libitum since the birds' arrival in January. We replaced the small seeds with large (confectionary) sunflower seeds on 26 February and again gathered 100 samples of each data type (28 February to 3 March). On 4 March, we once more provisioned the platform with small sunflower seeds and from 6-9 March repeated our data collecting procedures.

RESULTS

When we supplied small sunflower seeds, Pine Siskins attempted to obtain food from nearby Evening Grosbeaks in only 5–8% of cases (Table 1). In addition, siskins presented with small seeds rarely approached grosbeaks after fighting with conspecifics (Table 1). The tendency for siskins both to seek food from grosbeaks and to approach grosbeaks after fighting with conspecifics was slightly, but not significantly, greater after the birds had been exposed to large seeds than before this time ($\chi^2 = 0.74$, df = 1, P < 0.4; $\chi^2 = 2.08$, df = 1, P < 0.2; respectively).

When we introduced large sunflower seeds on 26 February, siskins arriving at the platform were unable to husk the seeds and moved rapidly about as if searching for seeds of a more suitable type. Within a few minutes, individual siskins began to approach and eat seed particles falling from the bills of grosbeaks. When we subsequently collected behavioral

TABLE 1. Interactions between Pine Siskins and Evening Grosbeaks presented with sunflower seeds of varying size and husking difficulty.

Interval (1978)	Seed type	Data type 1			Data type 2	
		n	Siskin seeks food from grosbeak	Grosbeak pecks siskin	n	Siskin seeks food from grosbeak after winning intraspecific fight
24–25 February	Small, soft-shelled	100	5	0	100	2
28 February–3 March	Large, hard-shelled	100	29	4	100	22
6–9 March	Small, soft-shelled	100	8	2	100	6

data, we found that siskins attempted to obtain food from grosbeaks in 29% of cases—a result that differed significantly from what occurred when we presented small seeds in earlier or later experiments (Table 1; $\chi^2 = 20.41$, df = 1, P < 0.001; $\chi^2 = 14.62$, df = 1, P < 0.001; respectively). Siskins also exhibited a markedly greater tendency to approach grosbeaks immediately after defeating conspecifics (22% of cases) than they did during the earlier or subsequent provisioning of small seeds (Table 1; $\chi^2 =$ 18.94, df = 1, P < 0.001; $\chi^2 = 10.63$, df = 1, P< 0.005; respectively). Regardless of seed size, grosbeaks in our study did not often respond aggressively to the siskins (Table 1), although Davis (1926) noted that grosbeaks commonly pecked at approaching siskins.

DISCUSSION

We seldom saw the behavior described by Davis (1926) when we provisioned our feeding station with small sunflower seeds, probably because Pine Siskins were able to husk these seeds. Conversely, when we presented large sunflower seeds, Pine Siskins were unable to feed independently and soon associated food availability with proximity to Evening Grosbeaks or Cassin's Finches. It was our impression, when the three species visited our feeding station in the spring of 1977, that Evening Grosbeaks dropped more food and responded less aggressively to approaching Pine Siskins than did Cassin's Finches. Perhaps for these reasons, siskins presented with large sunflower seeds appeared to forage most often near Evening Grosbeaks. Our results are consistent with field and laboratory studies of several species suggesting that individual birds adjust their food-searching methods and hunting locations to increase foraging efficiency (e.g., Royama 1970, Smith and Sweatman 1974, Wakeley 1978a, 1978b).

Pine Siskins that approached Evening Grosbeaks immediately after defeating conspecifics may have defended an area beneath the bill of a grosbeak as a resource, in which case a shift in social organization occurred from defense of an individual distance (when food was readily available) to defense of a specific position akin to territoriality (when accessible food was unevenly distributed and relatively scarce). However, it is also possible that the siskins defended an individual distance, and then happened to approach nearby grosbeaks. Weak support for the first alternative is provided by a small sample of filmed interactions, in which individual siskins repeatedly attacked conspecifics that attempted to feed beneath a grosbeak's bill and sometimes appeared preferentially to attack those siskins which were closest to the grosbeak's head (rather than those closest to the aggressor). Changes of social organization in response to varying ecological conditions have been documented in a number of vertebrate species (e.g. Carpenter and MacMillen 1976, Stacey and Bock 1978 and references cited therein).

Foraging commensalism between Pine Siskins and larger-billed birds may not be restricted to feeding stations. Turček (1956) noted commensalism of several small-billed species, including Eurasian Siskins (*Carduelis spinus*), with Red Crossbills (*Loxia curvirostra*) in spruce (*Picea* sp.) forests in Slovakia. He observed that (1956:31), "In summer and autumn, when the cones are not yet ripe, tits and Siskins can only extract seed from the cones with difficulty; they therefore follow the Crossbills to consume seeds from cones which they have opened."

The Pine Siskins in our study exhibited considerable flexibility of behavior, in that they (1) obtained food from larger-billed bird species when they could not husk seeds for themselves, (2) appeared to concentrate their foraging activity near that species which ostensibly provided greater benefit (more food) at less cost (fewer aggressive responses), and (3) may have altered their social organization in response to changes in food availability. We suspect that such opportunism might be of considerable survival value to Pine Siskins. We also think it possible that natural selection has favored flexibility per se in the foraging and social behavior of this cardueline species-a consideration that may be overlooked in attempts to determine the adaptive significance of behaviors presumed to be obligate.

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Department of Wildlife Science, UMC 52, Utah State University, Logan, Utah 84322. Accepted for publication 30 October 1978.