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Agonistic communication among wintering Purple Finches.—Agonistic displays traditionally have been viewed as exchanging information on the motivations and intentions of the signaler (Dawkins and Krebs 1978, but see Hinde 1981). Dawkins and Krebs (1978) argue there is no apparent advantage to an individual involved in a conflict to reveal its intentions or motivations. An individual may benefit most by lying about its intentions in order to deceive its opponent. This has led to the hypothesis that no true information should be communicated by agonistic signals. Other workers have retained a traditional view and argue that agonistic displays do communicate information and that individuals should have the ability to detect lying (Rhijin 1980, Hinde 1981).

Studies of agonistic communication have not provided complete support for either viewpoint. In reanalyzing data from 3 earlier studies, Caryl (1979) concluded there was no evidence that signalers revealed their intentions during agonistic displays. Other recent studies have reached the conclusion that agonistic displays *do* communicate the intentions (Bossema and Burgler 1980, Nelson 1984) or relative fighting abilities (Clutton-Brock and Albon 1979, Evans 1985) of the signaler. This study reports on information transfer during agonistic communication among Purple Finches (*Carpodacus purpureus*) in winter flocks. I describe the agonistic displays of the Purple Finch and the general course of agonistic encounters, and ask the following questions: (1) Do responses to signals vary with the type of display given? (2) Do displays predict the signalers' next acts? (3) Do winners and losers differ in their use of displays?

Methods.—Aggressive encounters were videotaped at a feeder at Elkhart Lake, Sheboygan County, Wisconsin, in January 1985. The Purple Finch is an irregular winter resident at the study site, and the finches came to the feeder in flocks of approximately 10–20 birds. A Panasonic video camera (Model WV-3400) was concealed in an enclosure 3 m from the feeder. All videotaping was done between 07:00 and 11:00 CST. The feeder, stocked with a mixture of thistle and small black sunflower seeds, was 1.5 m off the ground and had a 7 × 25 cm platform from which the finches could feed. The American Goldfinch (*Carduelis tristis*) was the only other species that visited the feeder regularly.

Finches fed on the platform, and aggressive encounters occurred over access to the seeds.

TABLE 1
RESPONSES OF PURPLE FINCHES TO DISPLAY TYPES

Display	Percent of responses					N
	Low Head Forward display	High Head Forward display	Bill display	Bill display with pecking	Retreat	
Low Head Forward	19	45	31	0	5	62
High Head Forward	0	16	68	0	16	56
Bill	0	0	42	10	48	118
Bill display with pecking	0	0	0	29	71	17

Through the use of slow-motion replay, the exact sequence of displays was determined for each encounter. Replays also made it possible to follow each individual throughout an encounter. None of the finches was colorbanded. An individual was considered to have lost an encounter (retreated) if it fled from the feeder or gave a submissive posture. An individual won an encounter if it remained on the feeder while its opponent retreated. Winners of encounters gained or retained access to the feeder. Individuals escalated an encounter if they responded to a display with another display. Encounters involving more than 2 individuals or any interspecific encounters were excluded ($N = 51$). I analyzed 351 encounters.

For each display given, I noted (1) the type of display, (2) the response of the recipient, and (3) the act of the signaler following the recipient's response. Recipients responded to displays either by giving a display, pecking the signaler, or by retreating. Signalers then either displayed, pecked their opponent, retreated, or remained on the feeder while their opponent retreated. For each display type, it was determined how frequently recipients used each response and how frequently each behavior was used by signalers in their next act. All statistical comparisons were done with a G-test.

Results.—I observed 3 types of agonistic display. In the Low Head Forward display the individual is in a horizontal position, with its neck partially extended and bill pointed at the opponent. In the High Head Forward display the finch is in a more upright posture with the neck extended towards its opponent; the bill is often open in a gape. In the Bill display the bird stands vertically, its body extended to its full height, pointing its bill downward at the opponent. The contestants sometimes grab each other's bills and alternate giving the Bill display. Finches may peck their opponents, at times repeatedly, while giving the Bill display. I observed no ritualized submissive posture, although birds did lean away and hop backwards from opponents.

Aggressive encounters were divided into the following categories: (1) Supplanting (7% of all encounters), which occurred when an individual flew directly at a finch on the feeder, and the perched individual fled immediately. The supplanting individual replaced the perched individual on the feeder. No displays were given during these encounters. (2) Single display encounters (70% of all encounters), in which birds directed a display at an opponent who immediately retreated. Most single display encounters were initiated with the Low Head Forward display (62%), with other initiating displays being the High Head Forward (21%), the Bill display (16%), and the Bill display with pecking (1%). (3) Multiple display encounters (23% of all encounters), in which both contestants displayed.

During multiple display encounters, recipients varied their responses to agonistic displays depending on the type of display given by the signaler ($G = 167.4$, df = 12, $P < 0.001$) (Table 1). Three major trends were apparent. First, displays differed in how effective they

TABLE 2

NEXT ACT OF SIGNALERS AFTER GIVING A DISPLAY

Display	Percent of next acts						N
	Low Head Forward display	High Head Forward display	Bill display	Bill display with pecking	Retreat	Win	
Low Head Forward	0	13	43	0	39	5	62
High Head Forward	0	2	46	4	32	16	56
Bill	0	0	17	9	26	48	118
Bill display with pecking	0	0	0	0	29	71	17

were in causing the recipient to flee. The Low Head Forward display was the least likely to be followed by fleeing (least effective), and the Bill display was the most effective. Second, pecking occurred only in response to the Bill display and Bill display with pecking. Thus, as displays became more effective, they also became riskier. When responding with a display, recipients always used a display of equal or higher intensity.

The next act of the signalers depended upon the type of display they had given initially ($G = 87.9$, df = 15, $P < 0.001$) (Table 2). Signalers were more likely to win an encounter after giving the Bill display. Signalers pecked at their opponent in their next act more as signal intensity increased.

Winners and losers varied in the frequency that they used each display. Winners used the Bill display most frequently; losers made greater use of the lower intensity displays ($G = 38.2$, df = 3, $P < 0.001$) (Table 3). Winners and losers also differed in how they escalated encounters. Losers were more likely than winners to escalate an encounter with a display equal in intensity to the preceding display rather than with one of higher intensity (36.4% vs 12.3%); winners were more likely than losers to use a display of higher intensity (87.7% vs 63.6%, $G = 7.7$, df = 1, $P < 0.01$). For example, in response to the High Head Forward display losers used the same display 85.7% of the time, while winners gave the Bill display 92.5% of the time. Losers rarely escalated encounters by using the Bill display.

Discussion.—The high percentage of single display encounters indicates that displays were highly effective in causing the recipient to flee. Each display type, however, had its own

TABLE 3

THE PERCENT EACH DISPLAY WAS USED AMONG ALL DISPLAYS GIVEN BY WINNERS AND LOSERS

Display	Percent use	
	Winners	Losers
Low Head Forward	20	31
High Head Forward	11	37
Bill	61	28
Bill display with pecking	8	5
N	145	108

effectiveness. In multiple display encounters, as displays became more effective, they also became riskier to use because of the increased probability of pecking by the recipient. Finches may have minimized risk by initiating encounters with the Low Head Forward display, the least risky display. If this initial display was ineffective, encounters showed a pattern of escalation with the displays being used becoming both more effective and more risky. Encounters might be viewed as a series of steps in which each contestant decided whether to give a display and escalate the encounter or to retreat, the winner being the finch most willing to risk injury and use the higher intensity displays. Purple Finch conflicts resemble Caryl's (1981) "war of nerves" in which costs (the risk of pecking) mount as the contest proceeds. The differences between winners and losers further support the conclusion that agonistic displays convey information. The way an individual uses displays and escalates an encounter provides information on its willingness to remain in the conflict and its likelihood of winning that encounter.

None of the displays proved to be good predictors of attack (pecking). A similar result led Caryl (1979) to conclude that agonistic displays do not convey the signaler's intentions. This conclusion, however, is based on the assumption that agonistic signals are meant to communicate the intention to attack. In this study agonistic displays are very effective in causing an opponent to flee. It is not surprising that the displays rarely predict attack: one cannot attack an opponent who is not there. My results suggest that agonistic displays convey the signaler's intention to remain in the contest and to risk a possible attack. Signalers may be kept honest in communicating their intentions by the risk of attack (Rhijin 1980).

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