

- LACK, D. 1954. The natural regulation of animal numbers. Oxford Univ. Press, London.
- McKILLIGAN, N. 1987. Causes of nesting losses in the cattle egret *Ardeola ibis* in eastern Australia with special reference to the pathogenicity of the tick *Argas (Percicargus) robertsi* to nestlings. *Aust. J. Ecol.* 12:9-16.
- NELSON, J. B. 1977. Some relationships between food and breeding in the marine Pelecaniformes, p. 77-87. In B. Stonehouse and C. Perrins [eds.], *Evolutionary ecology*. Macmillan Press, New York.
- OWRE, O. T. 1976. A second breeding colony of Waved Albatross *Diomedea irrorata*. *Ibis* 118:419-420.
- PETERSON, R. T. 1967. The Galápagos. *Natl. Geogr. Mag.* 131:541-585.
- RECHTEN, C. 1986. Factors determining the laying date of the Waved Albatross *Diomedea irrorata*. *Ibis* 128:492-501.
- RICKLEFS, R. E. 1969. An analysis of nesting mortality in birds. *Smithson. Contrib. Zool.* 9.
- VAN RIPER, C., S. G. VAN RIPER, M. L. GOFF, AND M. LAIRD. 1986. The epizootiology and ecological significance of malaria in Hawaiian land birds. *Ecol. Monogr.* 56:327-344.

The Condor 90:729-731
© The Cooper Ornithological Society 1988

ACCESS TO WINTER FOOD RESOURCES BY BRIGHT- VERSUS DULL-COLORED HOUSE FINCHES¹

MARY BOMBERGER BROWN AND CHARLES R. BROWN

Department of Biology, Yale University, P.O. Box 6666, New Haven, CT 06511

Key words: *Carpodacus mexicanus*; *dominance*; *foraging*; *House Finch*; *plumage maturation*; *social behavior*.

The adaptive significance of delayed plumage maturation in passerines is not yet understood, despite much discussion and speculation (Selander 1965; Rohwer 1975, 1978; Rohwer and Niles 1979; Rohwer et al. 1980; Flood 1984; Studd and Robertson 1985; Lyon and Montgomerie 1986). Rohwer (1986) recently suggested that female-like subadult plumages may confer competitive advantages to yearlings during the winter, when individuals compete for access to critical food resources. Virtually all empirical study of delayed plumage maturation in birds to date has been done during the breeding season, and there is little evidence to evaluate Rohwer's hypothesis that female-like plumages benefit individuals during the nonbreeding season. In this paper we report that female-like plumage in House Finches (*Carpodacus mexicanus*) is potentially advantageous during the winter, when males yield access to critical food resources in favor of females.

METHODS

Our observations were conducted at a feeder located in our backyard in Guilford, New Haven County, Connecticut, from 8 November 1987 through 8 January 1988. A cylindrical feeder containing four portholes

through which sunflower seeds were dispensed was placed about 2 m from a window through which our observations were made. The four perches were located on the same horizontal level, 90° apart. A total of 64 hr was spent observing the feeder, mostly from 08:00 to 12:00, EST, in all weather conditions. As a measure of access to food, we recorded which individuals actively supplanted others and which individuals deferred to others. A supplant was recorded whenever one bird approached a bird sitting on one of the perches, usually from the back, and displaced it. If the perched bird repelled the intruder, no supplant was recorded. We could not quantitatively record attempted displacements that were repelled, however, because many birds simply flew to the feeder and hovered near it. These individuals did not directly approach a specific incumbent but nevertheless were clearly prevented from feeding by birds already there, thus making criteria for assigning attempted (but unsuccessful) displacements overly subjective. If a displacement occurred, the incumbent usually left the perch without a fight upon the approach of the other bird. House Finches were scored as either "gray," meaning no red was visible in the plumage, or "red," those containing variable amounts of red plumage. For interactions between red individuals, we scored the birds in that given interaction as either roughly equivalent in amount of red plumage present, or differing in the amount of red. We did not establish categories of redness. About 50 House Finches of both red and gray plumages (in approximately equal frequency) used the feeder during the time of observations. All interactions were considered statistically independent. Although no birds were color-marked (some were recognizable by plumage differences), there appeared to be frequent turnover among

¹ Received 22 January 1988. Final acceptance 22 April 1988.

the individuals present and no single individuals dominated the data set.

RESULTS AND DISCUSSION

We observed 1,653 supplantings of one House Finch by another at the feeder. In 754 cases (45.6%) a gray-plumaged bird displaced a red-plumaged bird. Grays displaced grays 507 times (30.7%); reds displaced grays 267 times (16.1%); and reds displaced reds 125 times (7.6%). Plumage color significantly affected tendencies to displace other birds or be displaced ($\chi^2 = 8.76$, $df = 1$, $P = 0.003$). Gray-plumaged birds were clearly dominant to red-plumaged birds at the feeder. Among the displacements recorded between red birds ($n = 267$), in 163 cases (61.1%) a bird displaced an individual that had more red than itself. Seventy-three (27.3%) displacements occurred among individuals that had equal amounts of red. In only 31 cases (11.6%) did a red bird displace another red bird that had less red than itself.

These data indicate that gray-plumaged dominated red-plumaged House Finches at the feeder, thereby gaining greater access to food resources. Since the places to feed were limited to only four perches, deferring to a gray bird meant that a red bird probably lost real opportunities to feed. Furthermore, in competition among red-plumaged birds, those individuals with less red had an advantage in that redder birds deferred to them.

Our observations suggested that the red birds might take greater risks to feed than do gray birds. Whenever a disturbance occurred, such as the approach of a person, cat, dog, or other potential predator, the finches and House Sparrows (*Passer domesticus*) that also used the feeder, flushed from the feeder into a nearby hedge. Often, however, a single bird that had been at the feeder remained after all the others flushed. In these cases the individual remaining would alertly peer around from the perch but would continue husking sunflower seeds. We observed 124 instances of birds flushing from the feeder (and the ground underneath) in which one individual remained behind to feed. In 83 cases (66.9%) the bird remaining behind was a red-plumaged House Finch; in 39 cases (31.5%) it was a gray-plumaged House Finch; and in two cases (1.6%) it was a House Sparrow. These observations suggest that red-plumaged House Finches might be more likely to risk predation in order to remain at a food source to which they have gained access.

Displacement of red-plumaged by gray-plumaged House Finches probably reflected the red birds' active yielding to gray birds and not an inherent lack of aggressiveness by red birds. This is suggested by interactions among House Sparrows and red vs. gray House Finches. We observed red and gray House Finches displace House Sparrows 92 and 71 times, respectively. We observed House Sparrows displace red and gray House Finches 270 and 381 times, respectively. There was thus no evidence that red House Finches were inherently inferior in competing for foraging space, at least when their interactions with House Sparrows were considered.

Red and gray individuals in most cases correspond

to male and female House Finches, respectively. In contrast to Purple (*C. purpureus*) and Cassin's (*C. cassinii*) finches (Bent 1968), male House Finches during their first winter show at least some red in their plumage. The amount of red increases as males age (Michener and Michener 1931). Nevertheless, some males (presumably yearlings) exhibit very little red in their plumage, so little that we had trouble detecting it from 2 m away. Our observations indicate clearly that females are dominant to males in interactions at a winter food resource. To the degree that yearlings can mimic female appearance, they may succeed in "fooling" adult males into yielding to them too. Yearling males—those with less red—are dominant to older, redder males. The advantage of being gray (or as gray as possible) may be twofold: an individual wins directly in competing against adult males, and interference from all-gray females is reduced.

Why do bright adult male House Finches defer to females and to duller yearling males? Smith (1980) suggested that males of many monogamous species may be selected to defer to females and allow females access to critical resources that may be channeled into production of eggs or young in which the males have genetic interest. Brown (1984) adapted this idea into an explanation for delayed plumage maturation: yearling males can resemble females to gain access to resources reserved for females. But our observations reported here came from the nonbreeding season, and males should be less likely to defer to females in the winter. House Finches are relatively sedentary in Connecticut (see Elliott and Arbib 1953, Gill and Lanyon 1965), and a pair potentially could associate together year-round. There could possibly be an advantage for males in yielding access to females during the winter if pairs remain together for more than one winter. Gill and Lanyon (1965) reported instances of House Finches remaining pair-bonded throughout the winter and one case of a pair remaining together for two nesting seasons. However, at present we see no obvious benefit to males in yielding during the winter to females and yearling males (and possibly taking greater foraging risks as a result). Yet, whatever the reason, if males regularly defer to females during the winter, yearling male House Finches can gain an advantage by resembling females in appearance.

Our observations on House Finches in winter match closely those of Brown (1984) on Purple Martins (*Progne subis*) in summer, in which adult males yielded to females and yearling males. In the case of martins, the resource at stake was preferred perching space in a summer roost. As in House Finches, yearling male Purple Martins gained by being able to displace adult males and by being less likely to be displaced themselves by females. Further studies such as these are needed in both winter and summer to reveal possible advantages of female mimicry. The House Finch data reported here suggest that Rohwer's (1986) winter adaptation hypothesis for delayed plumage maturation should continue to be explored. These data also suggest that *Carpodacus* finches and especially the sedentary House Finch might be very appropriate species in which to examine theories based on both winter and summer adaptations.

LITERATURE CITED

- BENT, A. C. 1968. Life histories of North American cardinals, grosbeaks, buntings, towhees, finches, sparrows, and allies. Part one. U.S. Natl. Mus. Bull. 237.
- BROWN, C. R. 1984. Light-breasted Purple Martins dominate dark-breasted birds in a roost: implications for female mimicry. *Auk* 101:162-164.
- ELLIOTT, J. J., AND R. S. ARBIB, JR. 1953. Origin and status of the House Finch in the eastern United States. *Auk* 70:31-37.
- FLOOD, N. J. 1984. Adaptive significance of delayed plumage maturation in male Northern Orioles. *Evolution* 38:267-279.
- GILL, D. E., AND W. E. LANYON. 1965. Establishment, growth, and behavior of an extralimital population of House Finches at Huntington, New York. *Bird-Banding* 36:1-14.
- LYON, B. E., AND R. D. MONTGOMERIE. 1986. Delayed plumage maturation in passerine birds: reliable signaling by subordinate males? *Evolution* 40:605-615.
- MICHENER, H., AND J. R. MICHENER. 1931. Variation in color of male House Finches. *Condor* 33:12-19.
- ROHWER, S. 1975. The social significance of avian winter plumage variability. *Evolution* 29:593-610.
- ROHWER, S. 1978. Passerine subadult plumages and the deceptive acquisition of resources: a test of a critical assumption. *Condor* 80:173-179.
- ROHWER, S. 1986. A previously unknown plumage of first-year Indigo Buntings and theories of delayed plumage maturation. *Auk* 103:281-292.
- ROHWER, S., AND D. M. NILES. 1979. The subadult plumage of male Purple Martins: variability, female mimicry, and recent evolution. *Z. Tierpsychol.* 51:282-300.
- ROHWER, S., S. D. FRETWELL, AND D. M. NILES. 1980. Delayed maturation in passerine plumages and the deceptive acquisition of resources. *Am. Nat.* 115:400-437.
- SELANDER, R. K. 1965. On mating systems and sexual selection. *Am. Nat.* 99:129-141.
- SMITH, S. M. 1980. Henpecked males: the general pattern in monogamy? *J. Field Ornithol.* 51:55-63.
- STUDD, M. V., AND R. J. ROBERTSON. 1985. Life span, competition, and delayed plumage maturation in male passerines: the breeding threshold hypothesis. *Am. Nat.* 126:101-115.

The Condor 90:731-734

© The Cooper Ornithological Society 1988

AGE DIFFERENCES IN THE FALL DIET OF GREATER SNOW GEESE IN QUEBEC¹

JEAN-FRANÇOIS GIROUX² AND JEAN BÉDARD

Département de Biologie, Université Laval, Ste-Foy, Québec G1K 7P4, Canada

Key words: Age; diet; foraging behavior; Greater Snow Geese; Québec.

During their fall migration from the Canadian High Arctic to the Atlantic coast of the United States, Greater Snow Geese (*Chen caerulescens atlantica*) stop along the St. Lawrence River estuary where they feed in tidal brackish marshes (Lemieux 1959). No detailed information on the plants consumed by geese at this period is available. In this paper, we describe the diet of geese on their fall staging grounds and present evidence that adult and juvenile birds feed on different plant parts.

STUDY AREA AND METHODS

Samples were obtained from geese shot by hunters at Montmagny and Cap St. Ignace, 75 km NE of Québec City. In fall, geese along this shore of the river are

concentrated in two sections of marsh (sanctuaries) where hunting is prohibited. Hunting is conducted from permanent blinds located at the periphery of the protected areas (Giroux and Bédard 1986). The tidal marsh can be divided into two parts according to mean high water. The low marsh is dominated by *Scirpus americanus* with some *Zizania aquatica* var. *brevis*, *Sagittaria* spp., and *Eleocharis* spp. while the high marsh is covered by *Spartina pectinata* and *Carex paleacea* (Giroux and Bédard 1987). Most of the feeding occurs in the low marsh, the birds resting in the high marsh.

A total of 403 and 1,311 birds were examined in 1982 and 1983, respectively. Geese were classified as adults (including subadults and yearlings) or juveniles based on plumage coloration and were sexed by cloacal examination. Contents of the esophagus and proventriculus were collected, sorted by species and plant parts, dried at 70°C for 48 hr and weighed to the nearest 0.0001 g. Only geese with >0.05 g dry mass of food material were retained for analysis and data were expressed as the average percent dry mass (Prevett et al. 1979). Fiber content of the most important food items was determined by the neutral detergent fiber method (Goering and Van Soest 1970). The effect of age and

¹ Received 3 February 1988. Final acceptance 22 April 1988.

² Present address: Département des Sciences Biologiques, Université du Québec à Montréal, C. P. 8888, Succursale A, Montréal, Québec H3C 3P8, Canada.