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Responses of floaters to removal experiments on wintering chickadees

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Summary. In response to natural mortality in a local population of wintering black-capped chickadees, *Parus atricapillus,* high-ranked flock regulars are usually replaced rapidly by flock switchers, while low-ranked regulars are not replaced. A series of removal experiments was done to examine the replacement process. A large outdoor aviary was used to house the removed birds, all of which were returned to their flocks no more than 4 days after removal. Of 10 birds taken, all 6 of the high-ranked ones (3 males, 3 females) were replaced by flock switchers. All inserting switchers made sudden jumps in rank; each was seen to supplant regulars of its sex the day after removal. All 10 removed birds, including the 6 that had been replaced by switchers, regained their former status immediately upon release. The 6 switchers that had inserted into the artificial openings were all driven away, and stayed away from the flock for an average of 15 days. Four removed birds were not replaced. All were males from the bottom-ranked pair in their flock. This is consistent with field observations: of 58 low-ranked regulars disappearing naturally over 7 winters, none was replaced by a switcher, although to do so would be an apparent jump in rank for any switcher.

Introduction

Floaters typically differ from most other members of an avian population by (1) having lower rank than others of their sex and (2) having larger home ranges. Floaters have often been dismissed simply as strays or migrants, and thus relatively few studies have been done on their behavior or social organization.

Most studies that mention floaters were done in the breeding season. Many of these were concerned with whether or not territoriality regulates breeding densities, and thus were often aimed simply at demonstrating the existence of floaters, rather than looking at their behavior. They focus on replacement of territory owners either after removal experiments or where owners have died naturally (Power 1975; Thompson 1977; Saether and Fonstad 1981; Gullion 1981; Petrinovich and Patterson 1982; Hannon 1983). In several of these studies, replacement birds were unmarked, and often little was known about where they came from.

Winter floaters are now also recognized (Ekman 1979; Ekman et al. 1981). Ekman and his colleagues worked with willow tits (*Parus montanus*) which spend the winter in stable sedentary flocks. After autumn removal experiments, floaters settled and adopted "a sedentary habit" (Ekman et al. 1981, p 1).

Several *Parus* species may have winter floaters. Hinde (1952) and Drent (1983) each found that certain great tits (*P. major*) spend some time in one flock and some in another; the same may also be true in some blue tits, *P. caeruleus* (Colquhoun 1942) and marsh tits, *P. palustris* (Morley 1950). In the North American black-capped chickadee (*P. atricapillus*), wide-ranging individuals that move from flock to flock are frequently reported (Hartzler 1970; Glase 1973; Barash 1974).

For the past 7 winters, I have been studying the behavior of color-banded winter floaters, or flock switchers, in a population of black-capped chickadees in Massachusetts. There, winter chickadee flocks seem to be conposed of pairs of regulars (Smith 1984). Typically there is rank matching within these flocks, so that the alpha male is paired with the top-ranked female, number 2 with number 2, and so on. Thus the regulars in these winter flocks appear to be organized into a hierarchy of pairs. More birds start the winter in a flock than can breed locally; low-ranked pairs that survive the winter are usually driven away at flock break-up in the spring (Smith 1967, 1984).

Flock switchers are typically young, unpaired birds that range over 3–5 flock ranges and rank below all regular (i.e. sedentary) individuals of their sex in each of "their" flocks. When a member of a high-ranked pair disappears naturally, it is usually rapidly replaced by a local switcher, which may assume the rank and pair with the mate of the vanished bird (Smith 1984). By contrast, regulars that disappear from low-ranked pairs are usually not replaced (Smith 1987).

Natural mortality can provide only limited, ambiguous data. Indeed, I had no proof of mortality in my earlier, nonexperimental study – rather than replacing regulars that had died, some or all of my successful floaters might have driven them away to take over their positions in the hierarchies. Moreover, details of the replacement process can only be obtained when the exact time of disappearance is known. The obvious next step was to perform removal experiments. This paper reports on a series of removal experiments done with color-banded chickadee flocks in 1984/85 and 1985/86.

Methods

The study area, about 30 ha of mixed woods, old field, and residential area near Mount Holyoke College in western Massachusetts, is described in detail elsewhere (Smith 1984). I have color-banded chickadees there yearly since the fall of 1979, taking data at least once weekly from flock formation in late summer until after flock break-up the following spring.

Removal experiments involved mist-netting a chickadee and holding it in an outdoor aviary while observations were made on the rest of the bird's flock. The aviary consisted of two compartments each 3.7 m long, 1.8 m wide and 2.7 m high, each containing a wooden roosting box, and, for most of each winter, a cut, dense spruce tree. Each was provided with ad lib. sunflower seeds, suet, and water.

Chickadees to be removed were selected carefully. Only birds from completely color-banded flocks were taken. I also chose birds so that most were from their flocks' highest or lowest-ranked pairs.

Birds were removed only in the period of 1 Nov. to the end of Feb., to avoid any effects of late flock formation or early spring flock break-up. Since black-capped chickadees reportedly roost huddled together on very cold nights (Loery and Nichols 1985), and the aviary was outdoors and unheated, I only took birds when the forecast for the next four nights was for temperatures to go no lower than 0° F. Ten experiments were performed. All 10 birds were removed in the morning, to allow them to explore and settle before nightfall. Once a bird was in the aviary, aggressive interactions (mostly supplants and waits, see Smith 1984) were recorded among the rest of the bird's flock in measured blocks of time, so that interaction rates could be generated. I began timing when I encountered the right flock and ended when either it or I moved away; blocks of time ranged from 17 to 45 min. I made as many observations, both morning and afternoon, as weather and my time permitted. In each case they began on the afternoon of the day I removed the bird. In 7 experiments, observations were made in all 4 days of the removal period; in the other 3, I took interaction data on 3 of the 4 days. Four days after capture, the chickadees were returned to their flock territory and released.

Results

Of the 10 birds taken, 6 (3 males, 3 females) were replaced by flock switchers, and 4 others (all males) were not (Table 1). All 6 that were replaced were members of pairs in the top 2/3 of their flock hierarchies; those not replaced were all from their flock's lowest ranked pair. In order to find the probability of obtaining these results by chance, one could categorize the replacements as being in the top half or the bottom half of the hierarchy. Since the female replacement in the flock of six cannot be categorized accordingly, it should be omitted from this analysis. We then have 5 upper half openings all being replaced, while none of the 4 lower half openings were replaced. Applying the

Table 1. Removal experiments showing rank and sex of removed bird, size of its flock, dates held in captivity, which switcher (if any) inserted to replace the captive, and length of time that switcher stayed away from the flock after the release of the bird it had replaced

Removed bird	Flock size	Dates	Replacement	Replacement absence after release
# 1 female	8	11–29 to 12–02 '84	A1R KY	21
# 2 female	6	01–03 to 01–07 '85	A1R KG	23
# 1 female	4	02–14 to 02–18 '85	unbanded	?
# 2 male	8	12–02 to 12–06 '84	A1R GR	7
# 1 male	4	12–13 to 12–17 '84	A1R BY	24
# 1 male	8	01–10 to 01–14 '86	A1G OR[a]	1
# 3 male	6	11–24 to 11–28 '84	–	–
# 4 male	8	02–26 to 03–02 '85	–	–
# 2 male	4	11–18 to 11–22 '85	–	–
# 3 male	6	01–18 to 01–22 '86	–	–

[a] Replacement via complex substitution; all 5 other replacements were by simple substitution

Table 2. Some details of replacement, showing rank and sex of removed bird, its flock size, time (to the nearest quarter hour) between removal of a bird and the first observed supplanting of a regular of that sex by the inserting switcher, and the number of times during the removal period that the inserting switcher was seen supplanting the next highest regular in the flock, e.g., the first 5:0 means I saw the inserting switcher supplant the beta female 5 times, and the beta female was not seen to supplant the switcher at all

Removed bird	Flock size	Time to first observed supplanting by inserting switcher	Total interactions with nearest rival
# 1 female	8	26 h	5:0
# 2 female	6	27 h	3:0
# 1 female	4	$5\frac{1}{2}$ h	2:0
# 2 male	8	23 h	11:1
# 1 male	4	$30\frac{1}{4}$ h	7:0
# 1 male	8	22 h	9:0
	Average:	22.3 h	

two-tailed *G*-test with Williams correction, the birds' responses to high and low ranked openings was significantly different at the 0.02 level.

Five of the 6 replacements were by simple substitution, in which the inserting switcher assumes the rank and associates with the mate of the bird it replaces. The other (of an alpha male from an 8-bird flock) was by complex substitution; here the beta male switched partners and became the top-ranked bird; the inserting switcher then took over the vacated beta position, associating with the second-ranked female.

On two occasions I saw the switcher that would replace a bird associating with its flock less than 2 h after I had removed it. In one case, an inserting female supplanted her new rival (i.e. the regular ranked just below the position the inserting bird was taking over). In the other case (an inserting male), however, insertion had clearly not yet occurred, since the switcher that was to take over as beta male was supplanted by the flock's third-ranked male. Nevertheless, by the next day, all six replacements were established; indeed, the average interval between removing a bird and seeing its replacement supplant a regular of its sex was 22.3 h (Table 2). This represents a radical change in rankings, since switchers before insertion always rank below regulars of their sex. Moreover, I saw no evidence of an inserting switcher gradually moving up through the ranks, but rather a sudden complete jump in rank.

In the afternoon after each removal, I recorded the behavior of the removed bird's mate. Only 3 of the 4 low-ranked males had a surviving mate at the time of removal; none was seen to display any particular response to their mate's absence. For the high-ranked birds, the response was apparently mixed. All four "widowed" members of the alpha pairs were seen wandering away from the rest of their flock giving loud and repeated *dee dee dee* calls in apparent search for their mates. Of the four seen doing this, only two were from pairs that had bred together before. Neither beta mates, including one from a pair that had bred together the previous summer, were seen doing this.

During all 10 removal periods, I obtained rates of aggressive interactions among the remaining flock members (Table 3). For experiments that resulted in replacement, I calculated the number of aggressive interactions involving the inserting switcher per bird per minute. For male replacements, this averaged 0.026 switcher-interactions/bird/min, whereas for female replacements, it averaged only 0.009 switcher-interactions/bird/min. This difference, while not significant on analysis with the Mann-Whitney *U*-test ($P=0.10$), is nevertheless consistent with my observations on natural replacements.

Total interactions/bird/min, i.e. those between any 2 birds associating with the flock, averaged 0.022 for female replacements and 0.037 for male replacements, for an overall average of 0.029 interactions/bird/min. By contrast, the average interactions/bird/min during experiments involving no replacement was only 0.004 interactions/bird/min. When these two rates are compared by the Mann-Whitney *U*-test, the interaction rate for replacements is significantly greater than that for nonreplacements at the 0.02 level.

Upon release, all 10 birds regained their former rank right away: within 49 h of release, I saw all 10 supplant or chase the bird ranked just below them before capture: for 3 birds I saw this within 35 min of release. The 6 switchers that had settled were driven away from the flocks where they had inserted; on two occasions the released bird was seen chasing the switcher that had replaced it within 20 min of release. Subsequently, most of these 6 switchers reduced their home ranges, thus avoiding the flock where they had temporarily inserted. It took them an average of 15.2 days before they once again included those flocks in their home range (Table 1). Five of the 6 high-ranked birds used in removal experiments survived the winter; all obtained local breeding territories the following spring. Also, 2 of the 6 switchers (1 male, 1 female) that had replaced captive birds inserted later into natural openings and bred locally.

Table 3. Interaction rates after removal, showing total interactions per minute, interactions per bird per minute, and, where replacement occurred, interactions involving the inserting switcher per bird per minute

Removed bird	Replaced?	Int/min	Flock size	Int/bird/min	Inserting switcher int/bird/min
# 1 female	yes	0.147	8	0.018	0.010
# 2 female	yes	0.048	6	0.008	0.005
# 1 female	yes	0.156	4	0.039	0.011
			Averages:	0.022	0.009
# 2 male	yes	0.211	8	0.026	0.019
# 1 male	yes	0.218	4	0.055	0.036
# 1 male	yes	0.232	8	0.029	0.022
			Averages:	0.037	0.026
# 3 male	no	0.009	6	0.001	–
# 4 male	no	0.015	8	0.002	–
# 2 male	no	0.040	4	0.010	–
# 3 male	no	0.020	6	0.003	–
			Average:	0.004	

A number of chickadees died of natural causes each year of the study. Over 7 winters, 37 high-ranked birds vanished between October and March, i.e. before spring flock break-up began. Fourteen of these represent 7 intact pairs. Since switcher-switcher pairs are not normally formed (Smith 1984), the second member of a pair to die would not be replaced, and the switcher that had replaced the first member would be forced to resume switching; hence these 14 deaths did not provide permanent openings for switchers. However, of the 23 single high-ranked birds lost, 22 were replaced by switchers, 19 of which were banded. By contrast, 58 low-ranked regulars vanished over the same period, and none was replaced by switchers. Significantly, only those birds that end the winter as members of pairs in the top two-thirds of their flock hierarchies are normally assured of obtaining local breeding territories. The problem of why any young bird would become a low-ranked regular at flock formation is discussed elsewhere (Smith 1987).

One high-ranked bird that vanished naturally went unreplaced. In mid-November, 1985, the third-ranked female from a 10-bird flock disappeared, and her mate went unpaired until the flock break-up in April, when he acquired an unbanded mate and bred locally. For unknown reasons the slot thus remained unfilled for over 4 months, although several banded female flock switchers (and, to the best of my knowledge, no unbanded ones) were in the area throughout that period. All other such slots were filled rapidly by switchers.

Discussion

The data in Table 1 support the hypothesis that switcher insertions occur in response to high-ranked birds' disappearing, rather than that successful switchers move up and force high-ranked regulars out of their flocks. While earlier, nonexperimental data show that some apparently vulnerable chickadees can maintain rank with plenty of switchers available to oust them (e.g. in 1983/84, a broken-legged chickadee remained alpha male of an 8-bird flock all winter), what we do not know is whether the birds that were replaced naturally had been, in some way, even more vulnerable. However, the current data now show that switchers can and do respond to artificially created openings by insertion. It seems likely that this is, in fact, the usual pattern.

Both for natural vacancies and in the removal experiments, switchers were selective as to which openings they settled into, i.e., they only replaced members of high-ranked pairs, while low-ranked openings remained unfilled. Yet regulars always rank above every switcher of their sex, so to move into a low-ranked slot would, in fact, be an increase in rank for any switcher. Why do switchers so consistently ignore these low-ranked openings?

Two factors are probably important in the answer. First, as mentioned above, very few birds ending the winter as low-ranked regulars will get to breed locally; most get driven away at spring flock break-up. Second, unlike any regular, switchers lack pair bonds. These pair bonds apparently lock low-ranked regulars into their position near the bottom of their hierarchies (Smith 1984); unpaired switchers, by contrast, are free to move into any newly vacated slot. A switcher that moved into a low-ranked slot would give up this freedom in exchange for a minimal gain in rank and a very poor chance of breeding locally next spring. Only those switchers that wait for a high-ranked opening will have any real chance of joining the local breeding population in the spring.

The process of insertion into high-ranked openings in my study area is a very rapid one: switchers had supplanted their new rivals an average of only 22.3 h after the openings were created (Table 2). Very rapid insertions are probably common in the breeding season (Smith 1978; Hansen and Rohwer 1986). However, in the nonbreeding season, speed of replacement is likely much slower. Indeed, the speed I report for nonbreeding season replacements may well be unusual. My study area supports an unusually high switcher density (Smith 1987), possibly in part because of its many feeders. With such a high density of switchers, competition among them may be artificially raised, so each available slot will be "snapped up" within hours of becoming open. Perhaps at lower, more normal switcher densities, the replacement process would be considerably slower, especially for the middle-ranked positions. It is interesting that the one case of an upper-ranked slot remaining unfilled for over 4 months was indeed such a middle-ranked slot.

All 10 experimental birds regained their original rank immediately upon release. This fits well with data reported for male red-winged blackbirds, *Agelaius phoeniceus,* by Beletsky and Orians (1987). They found that male redwings removed from their territories for up to 48 h could recover their territories, but that those removed for a week could not. It would be interesting to see how long a chickadee must be kept from its flock before losing its ability to regain its original status. Possible factors that might affect the length of this period include the age, sex, and rank not only of the removed bird but also of its mate.

Most chickadee populations in relatively decent habitat will have at least low switcher densities in most winters; e.g. Hannon (personal communication) has found switchers in a northern Alberta black-capped chickadee population. However, populations in very poor habitats, or better habitats in very harsh winters, may well have no switchers at all. Very likely in such switcherless areas, pair bonds would be broken after a high-ranked regular vanished, with the vacant slot being filled by the next-highest ranked bird. I have seen this to a limited extent in complex substitutions; however, if no floaters are available, a domino effect may occur, in which many regulars of the sex that died break their pair bonds and move up one place in the hierarchy. It would be interesting to see whether, in the absence of switchers, regulars do move into higher-ranked slots, and, if so, how far down the ranks the domino effect progresses.

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