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SOCIAL DOMINANCE IN YOUNG WHITE-THROATED SPARROWS: EFFECTS OF EARLY SOCIAL EXPERIENCE AND THE UNSTABLE PERIOD

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ABSTRACT.—I examined the influence of early social experience on winter dominating ability in White-throated Sparrows (*Zonotrichia albicollis*). Eleven sparrows from four broods were hand raised to independence, housed in flocks with their brood mates for 8 to 9 weeks, placed in isolation or in a flock of six for an additional 17 weeks (the experimental phase), and then tested for "final dominance" in one of three juvenile flocks consisting of unfamiliar hand-reared birds and wild-caught birds. The mass of a nestling relative to its brood mates was not correlated with its final dominance, and no dominance interactions were observed between nestlings. Similarly, although an unstable period occurred in the brood-mate flocks during which dominance relationships fluctuated greatly from day to day, neither dominance status nor total number of dominance interactions in the brood-mate flocks was correlated with final dominance. In contrast, social conditions imposed during the experimental phase appeared to influence final dominance strongly. Three of five isolates achieved the top rank in final flocks, sparrows from the experimental flock were all of low rank, and wild-caught sparrows attained intermediate rank. These results suggest that the social conditions experienced by juvenile White-throated Sparrows before they leave the breeding ground and during fall migration might have a lasting effect on their dominance status and, thus, their survival in winter. *Received 14 October 1994, accepted 5 April 1995.*

SOCIAL DOMINANCE, the ability of an individual to gain access to resources by supplanting conspecifics, has profound behavioral and ecological consequences in birds. Dominant birds enjoy increased reproductive success in the breeding season (e.g. Davies 1992, Marzluff and Balda 1992) and benefit by feeding more efficiently or safely (Schneider 1984, Hogstad 1988) in winter. Dominance also appears to confer higher survival (Desrochers et al. 1988, Piper and Wiley 1990a; but see also Hogstad 1987).

The recognition of the ecological importance of dominance has led to increased interest in the factors that lead to high dominance status. Age (Arcese and Smith 1985, Piper and Wiley 1989, 1991) and various morphological attributes such as large size (Baker and Fox 1978) and body coloration (Rohwer and Rohwer 1978) have been found to confer the ability to dominate opponents. Researchers also have noted that a variety of situational factors—such as hunger (Popp 1987, Cristol 1992), familiarity with the site of the interaction (Eden 1987, Dearborn and Wiley 1993), and the influence of third individuals (Chase 1982)—affect the outcome of dominance interactions.

Although many studies have reported correlates of dominating ability, relatively few have emphasized the important point that morphological attributes and subtler situational factors together often fail to explain the variability in dominating ability found in animals. While some of the unexplained variability in dominance certainly is attributable to a failure to measure all potential correlates or to sampling error, there seems to be a palpable "missing component" in dominating ability.

Genetic and developmental influences are potentially strong determinants of dominance that might explain its missing component. A genetic influence on dominance (e.g. Craig et al. 1965), unless it was linked to some easily-measured morphological character in adults, would not be detectable in adults and, yet, would produce consistent differences in dominating ability. Similarly, an effect of rate of development or early social environment on dominating ability (Arcese and Smith 1985, Drummond and Osorno 1992, Schwabl 1993) would be un-

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detectable to those observing dominance in adults, but might reduce the accuracy with which observers could predict dominance status in adult groups.

The White-throated Sparrow (*Zonotrichia albicollis*) is a tractable species for an investigation of possible genetic or developmental origins of dominating ability for at least four reasons. First, White-throated Sparrows are easily hand-reared and maintained in captivity (Dearborn and Wiley 1993). Second, a thorough search has shown that intrinsic and situational correlates together explain only about 50% of the variability in dominance status in free-living White-throated Sparrows (Piper and Wiley 1989, 1991). Third, much of the unexplained variability in the dominance of this species seems to result from a strong tendency for individuals to retain a particular dominating ability throughout their lives (Piper and Wiley 1989, 1991), which indicates that dominating ability might become largely fixed at some level before an individual's first winter. Finally, dominance status is significant ecologically in wintering White-throated Sparrows because it influences factors such as likelihood of predation (Schneider 1984, Piper 1990a), use of space (Piper and Wiley 1990b, Piper 1990b), rate of singing (Wiley et al. 1993), and survival rate from one winter to the next (Piper and Wiley 1990a).

In this study, I examine the potential influence of social experience during the first six months of life on dominating ability in hand-reared White-throated Sparrows. Although the main focus here is on the importance of early agonistic encounters on subsequent dominating ability, the use of hand-reared broods also makes it possible to take a preliminary look for genetic effects.

METHODS

The treatment of the birds in this study represented a compromise between efforts to approximate social conditions experienced by free-living birds and the need to look for effects of social conditions on dominating ability. The experiment can be subdivided into four phases. First, 11 sparrows were hand reared to independence. Second, the birds were housed in four separate aviaries by brood. Third, birds were moved to new aviaries in which they resided alone or in a flock of six hand-reared sparrows (the experimental phase). Finally, the birds were placed in one of three flocks that contained: isolates; birds from the flock of six; or wild-caught birds. In these three "final" flocks, dominating ability in winter was assessed.

I collected nestlings during June 1992 from an overgrown 40-ha tract near Paradise, Michigan that had been clear cut two to three years previously. Nests of White-throated Sparrows were located by flushing incubating females or by observing trips of adults to and from nests during nest building and feeding of nestlings. Four complete broods of nestlings five to eight days of age were taken on 21 June (brood of two), 24 June (brood of three) and 25 June (one brood of two and one brood of four), fitted with colored leg bands, and placed in artificial nests. Young White-throated Sparrows were hand fed hourly on a mixture of ground-up mealworms and nestling mix (composed of eggs, carrots, dog food, chicken laying mash, turkey starter mash, wheat germ, rice and molasses) until independence. When they were 7 to 14 days old, all 11 sparrows were driven overnight from Paradise, Michigan to Bloomington, Indiana, where they remained for the duration of the study. At fledging (day 8 or 9 after hatching), sparrows were placed for one to two days in 30 × 30 × 20 cm boxes with their brood mates until day 10. I then removed sparrows from the company of their brood mates and placed them in 1 of 11 cubic wire-mesh cages measuring 40 cm on a side. Opaque barriers were placed between adjacent individual cages so that sparrows could not see each other but could see human activity occurring in the room. From day 16 on, each visually (but not acoustically) isolated sparrow was provided *ad libitum* with water, dry nestling mix, soaked millet, and crushed grapes; each was given four to six mealworms per day. Beginning day 30, hand feedings were carried out with decreasing frequency until, from days 42 to 46, the sparrows fed themselves completely. Between days 24 and 46, all sparrows were exposed to 20 to 30 min of clear adult song during the morning (0700–0800 CST) and evening (1800–2000).

When sparrows became capable of feeding themselves (at 46 days of age; 29 July–5 August), they were removed from individual cages and placed with their brood mate(s) in an outdoor aviary measuring 6 × 2.5 × 2.5 m. Brood-mate flocks were maintained for eight or nine weeks (depending on age of brood).

On 22 September, after the hand-reared sparrows had reached three months of age, 6 of the 11 (1 each from the broods of 2, and 2 each from the broods of 3 and 4) were removed from brood-mate flocks and placed in a single aviary unfamiliar to all of them; this comprised an "experimental flock." The remaining five sparrows from four broods were placed alone in unfamiliar aviaries and constituted "isolates." All isolates and the birds in the experimental flock were separated from the nearest aviary containing hand-reared birds by at least one intervening aviary (thus 2.5 m), but were not visually or acoustically isolated from other White-throated Sparrows, or from wild birds that landed on the roofs or fed near the sides of aviaries. The experimental phase lasted for 120 days.

From 6 through 8 November, I used treadle traps to capture eight wild White-throated Sparrows in Bloomington, Indiana, with the aim of comparing their dominating abilities with those of hand-reared birds. Seven of the wild-caught birds were first-winter birds, as indicated by skull pneumatization (see Wiley and Piper 1992), and the eighth (Orange-Blue) was a second-winter or older bird. Before being housed with hand-reared sparrows, wild-caught individuals were randomly assigned to four empty aviaries in pairs. Aviaries containing wild-caught individuals in all cases were adjacent to aviaries containing the experimental flock or isolates. Birds in adjacent aviaries could easily see, hear and interact with each other and often flushed to cover as single flocks.

On 20 January, when the hand-reared sparrows were about seven months of age, three new final flocks consisting of seven, seven and five birds were created as a means of assessing the dominating abilities of hand-reared sparrows against each other and against wild-caught birds. Each final flock of seven birds consisted of two hand-reared sparrows from the experimental flock, two isolates that had never encountered each other previously, and three wild-caught birds that had never interacted previously (except possibly before capture, 10 weeks earlier). The final flock of five birds was similar to the flocks of seven except that it contained only one isolate and only two wild-caught birds. As in all previous phases, none of the sparrows was put into an aviary in which it had resided previously. The unflattened wing-chord lengths of all 19 sparrows in aviaries was measured to the nearest 0.5 mm.

I observed dominance interactions of the sparrows throughout the experiment, from hand rearing through the final flock phase. All 11 hand-reared sparrows remained tame throughout the nine months of the experiment, and I observed them from as close as 0.5 m while sitting quietly in the aviaries during the brood-mate and experimental phases. However, all final flocks were observed through small glass windows from a dark room so that wild-caught birds were not disturbed by the observer. Dominance interactions of six kinds were recorded (see also Piper and Wiley 1989, 1991): (1) supplantations (gradual displacements of one bird by a second, the dominant); (2) attacks (rapid displacements); (3) pursuits (chases that occurred on ground or in air); (4) fights (stereotyped beak-to-beak interactions wherein both birds fluttered upwards off of the ground until one, the subordinate, fled); (5) hold-offs (subtle interactions where one bird, considered the dominant, held its ground despite the close approach of a second); and (6) active pecking of an opponent. All of these interactions except active pecking, which is rarely seen, have been shown to give reliable indications of dominance between pairs of adult White-throated Sparrows in winter (Piper and Wiley 1989, 1991). I also recorded all instances of subsong, plastic song and crystallized song by hand-reared and wild-caught sparrows and noted the context in which song occurred.

RESULTS

No dominance interactions were observed among nestlings during 22.2 h of hand feedings. Indeed, nestlings showed no recognition of their brood mates as conspecifics, but instead treated them simply as obstacles between themselves and food. Dominance interactions were also lacking in the one to two days (12.5 h of observation) after they fledged and before they were placed in their individual cages, during which time they hopped awkwardly around in boxes shared with brood mates, although they occasionally gaped at and begged from brood mates. The only exceptions were one clear peck by eight-day-old fledgling Orange to the head of its brood mate, Light Blue, and two similar pecks by Orange to the head of its other brood mate, Light Green, on the following day.

In the few hours after the sparrows were removed from visual isolation and placed with their brood mates in large outdoor aviaries, their agonistic behavior followed a consistent pattern. Dominance interactions began to occur almost immediately, but the very first interactions often consisted of light pecks to the heads of opponents (4 of 11 of first interactions between pairs of brood mates) in addition to the supplantations, attacks, fights, hold-offs, and pursuits that characterize adults. Altogether, the proportion of pecks to the heads of others was 10.1% (23 of 227 dominance interactions) on the first day with brood mates, but only 1.3% (4 of 311 pecks) over the next three days ($G = 22.5$, 1 df, $P < 0.001$). I gathered no data on spacing behavior, but it seemed clear that the sparrows in brood-mate flocks approached each other more closely than do adults in winter.

The most unusual pattern observed in dominance relationships in brood-mate flocks was their striking instability over time, which was evident in 7 of the 11 total relationships, was found in all four brood-mate flocks and involved all individuals except Light Blue (Fig. 1). Instability took two general forms: flip-flops in dominance and prolonged high rates of reversals. One of the clearest examples of flip-flops occurred between Red and Blue-left. In this dyad, Red was clearly dominant during the first 16 days of observation, subordinate for the next 17 days, dominant for another day, subordinate for 2 days, and then dominant for the final 20 days of observation (Fig. 1). Thus, four observed flip-flops occurred in this dyad. The second form of instability, a prolonged high rate of reversals, occurred most clearly in the case of Dark Green and White. Although White was clearly dominant for the first six days, Dark Green became mostly dominant thereafter but continued to lose many interactions to White in their remaining seven weeks together. Instability of this kind occurred also in the Black/Blue-right, Yellow/Purple, and Yellow/Black dyads. Some relationships (e.g. Black/Blue-right; Fig. 1) exhibited both forms of instability. However, a few relationships (e.g. Light Green/Light Blue; Fig. 1) formed rapidly and remained stable throughout the seven to eight weeks in brood-mate flocks.

The unstable period was unusual not only because of flip-flops and reversals, but also because energetic dominance interactions were quite common. Most obvious among these interactions were pursuits, which constitute less than 1% of interactions among adults in winter (Piper and Wiley unpubl. data), but comprised 19.4% of interactions in the brood-mate period (n = 2,310 interactions), 15.7% in the experimental phase (n = 1,284) and 11.8% in the final flocks (n = 406; hand-reared birds only). Similarly, fights made up 1.6, 1.0, and 0.2% of all interactions, respectively, in the brood-mate, experimental, and final flocks.

Although there was instability during the first 4 days of the experimental flock (see Fig. 2 and Table 1), dominance relationships in the experimental flock assumed a stable form within 5 days and remained stable for 120 days (compare Figs. 1 and 2). Two of the 15 pairs of sparrows were observed in both the brood-mate and experimental flocks, and exhibited the respective instability and stability characteristic of each phase (compare Yellow/Blue-right and Orange/Light Green dyads in Figs. 1 and 2).

When the isolates, experimental flock birds and wild-caught birds were placed into the final flocks, they quickly established stable dominance relationships (Tables 2–4), as in the experimental flock. The resulting hierarchies were linear with one exception: Red, the fourth-ranked bird in Flock 2, was clearly dominant to Light Blue, which was otherwise the top-ranked bird. A wild-caught bird, Purple-Orange of Flock 2, fell suddenly from third to seventh rank on about 9 March (Table 3), but this sudden change in rank did not introduce nonlinearity into the dominance hierarchy of its flock.

I found no association between the social experience acquired by hand-reared sparrows in brood-mate flocks (i.e. in the second to fourth months of life) and their "final dominance" (a bird's dominance status in its final flock). Final dominance (expressed as percentage of opponents dominated) was not positively correlated with the total number of dominance interactions in which a sparrow engaged ($r = -0.26$, $n = 11$, $P = 0.44$, two-tailed Pearson correlation), the number of times it dominated opponents ($r = -0.40$, $n = 11$, $P = 0.22$), or the estimated proportion of interactions in which it had been dominant in its brood-mate flock ($r = -0.34$, $n = 11$, $P = 0.31$).

In contrast to social experience in brood-mate flocks, social experience during the experimental flock/isolate phase of the experiment appeared to influence final dominance. In each final flock, the top-ranking bird was an isolate, wild-caught sparrows were ranked immediately behind (ranks 2 and 3 in the flock of five; ranks 2–4 in the flocks of seven), and no sparrow from the experimental flock achieved a rank in the top half of a final flock (Tables 2–4). In the two flocks containing two isolates each, the isolates not attaining the top rank were ranked fifth of seven birds and seventh of seven birds.

Since I had no hypothesis *a priori* regarding the effect that social conditions during the experimental phase would have on winter dominance, statistical analysis of the patterns of dominance in the final flocks was not straightforward. The situation was further complicated by the fact that size, a known correlate of dominance in White-throated Sparrows (see Piper and Wiley 1989, 1991), differed among the experimental groups (mean wing chords for isolates, experimental-flock birds, and wild-caught birds, respectively: $\bar{x}$ = 67.5 ± SD of 1.8; 68.3 ± 2.8; 71.4 ± 0.9). An analysis of covariance, using final dominance (proportion of all opponents dominated) as the criterion (dependent) variable, treatment as the predictor (independent) variable, and wing chord as a covariate revealed a significant effect of treatment and a nearly significant effect of wing chord on final dominance (Table 5). This result is not dependent upon the presence of wild-caught

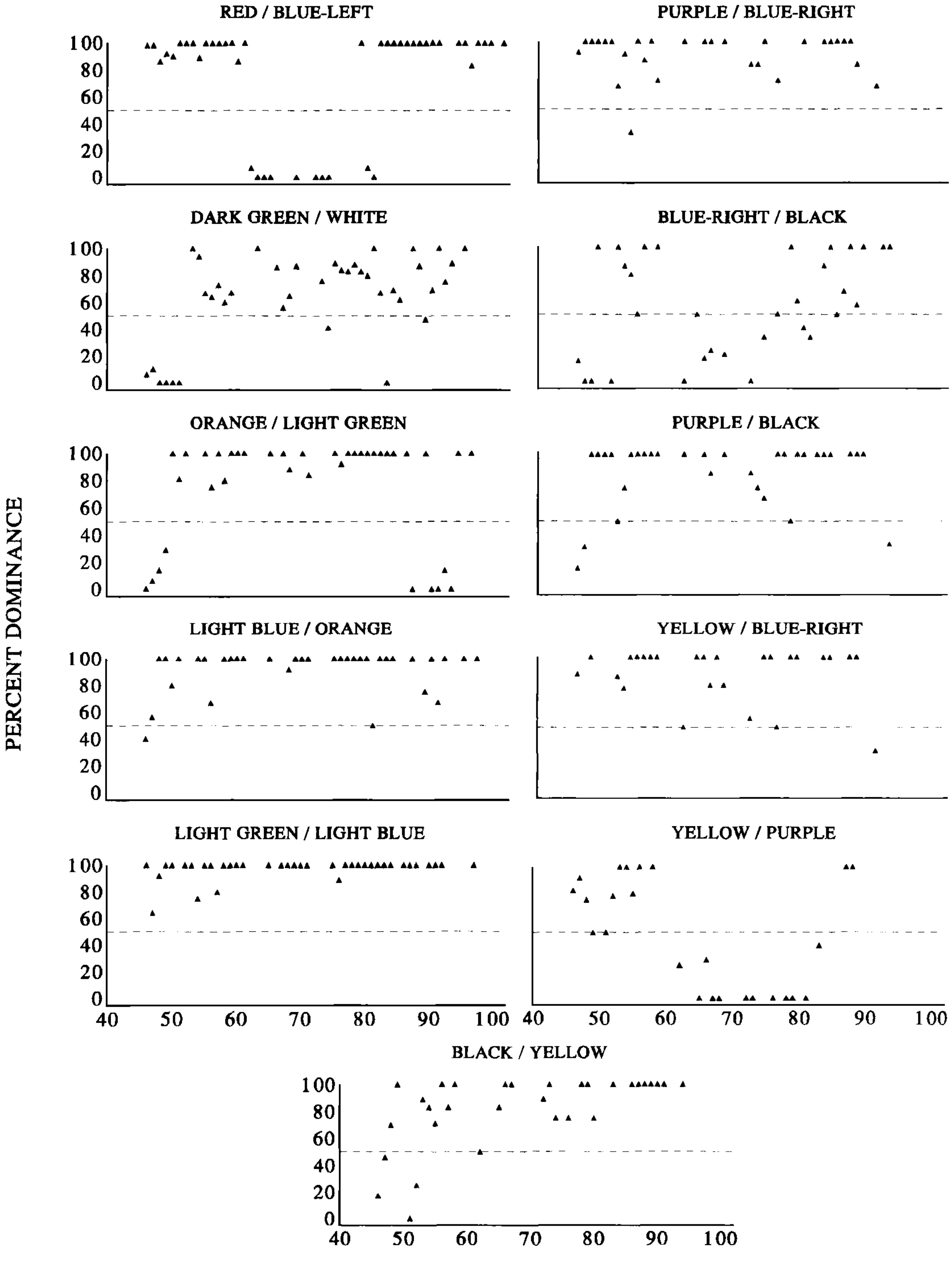

Fig. 1. Daily percentages of dominance interactions won (by individual listed first) plotted against age for all 11 dyads of hand-reared brood mates in four flocks. Flocks comprised: (1) Red and Blue-Left; (2) Dark Green and White; (3) Light Green, Orange, and Light Blue; (4) Purple, Blue-Right, Black, and Yellow. Each data point represents two or more interactions. Dashed line indicates 50% dominance (equal number of

birds in the sample; analysis of covariance excluding all wild-caught birds yielded a statistically significant effect of treatment on final dominance ($F_{1,8} = 5.33$, $P = 0.050$; $n = 11$).

Although samples were small, I looked for evidence that final dominance was affected by some genetic, maternal, or early developmental factor during the nestling phase. The three top-ranked isolates in the final flocks were all from different broods, and there was no significant tendency for sparrows from the same broods to attain the same final dominance ($r = 0.25$, $n = 11$, $P = 0.55$, ANOVA). Moreover, an examination of nestling mass revealed no significant tendency for heavy nestlings (those consistently heavier than their brood mates at daily weighings) to achieve higher final dominance status; in fact, lighter nestlings tended to become dominant, though not significantly so ($r = 0.56$, $n = 11$, $P = 0.07$; two-tailed Pearson correlation).

Singing was frequent among the hand-reared sparrows, especially in the brood-mate and experimental flocks. All 11 hand-reared sparrows sang in the brood-mate flocks (range of 3–16 times observed singing; $\bar{x} = 8.5 \pm 5.0$), and all birds but Dark Green (an isolate) were observed singing during the experimental flock/isolate stage as well. The songs observed fell into two main categories: (1) soft, gurgling, whistled subsong emitted with the bill closed during normal activities (e.g. foraging on the ground); and (2) loud whistled plastic song sung with the bill open and often from a high perch. On many occasions, plastic song occurred immediately before, during, or after dominance interactions. When a given bird sang many examples of plastic song over a short period, the songs always varied greatly and contained many truncated notes and phrases. No crystallized song was heard from any hand-reared sparrow during any stage of the experiment. (Only one wild-caught bird, Purple-Orange, sang crystallized song.)

The close temporal association between song development and the unstable period suggests a possible link between singing and dominance. However, there was no evidence for a correlation between frequency of singing in the brood-mate flocks and either dominance in brood-mate flocks ($r = -0.01$, $n = 11$, $P = 0.97$; Pearson correlation) or final dominance ($r = 0.20$, $n = 11$, $P = 0.56$), nor was there a correlation between frequency of singing and the degree of instability in dominance relationships with opponents ($r = -0.33$, $n = 11$, $P = 0.32$; instability measured as SD of daily percentage dominance scores averaged across all opponents). On a finer scale, there was no evidence that singing on particular days was related to dominance status on those days. For 55 bird-days of singing in brood-mate flocks (involving all 11 birds), 27 occurred on days when singers achieved percentage dominance scores (percentage of all interactions with opponents in which bird was dominant) greater than the median for that dyad, and 28 occurred on days of submedian dominance ($P > 0.5$, binomial test, two-tailed).

It is plausible that birds that sang at a young age also were advanced in terms of social development and might have dominated opponents more successfully than birds whose first songs occurred later. This also was not the case for dominance in brood-mate flocks ($r = -0.08$, $n = 11$, $P = 0.80$) or final dominance ($r = -0.56$, $n = 11$, $P = 0.07$). Indeed, birds with high final dominance scores tended to be those that began singing latest in the brood-mate flocks, although this trend was nonsignificant.

DISCUSSION

In spite of the unnatural ways in which the sparrows were housed and reared, all obvious aspects of the behavior of the hand-reared sparrows were similar to those normally observed in wild sparrows. All 11 hand-reared birds fed, preened, gave alarm and contact calls, and fled to cover at the approach of bird-eating hawks (*Accipiter* sp.), just like wintering adults (Piper and Wiley 1989, 1991, Wiley et al. 1993) and like the wild-caught birds with which they were ultimately housed. The occurrence of subsong

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interactions won by each member of dyad). By virtue of their high frequencies of flip-flops and reversals, dominance relationships among juveniles in brood-mate flocks were extremely unstable in comparison to relationships in experimental flock (see Fig. 2).

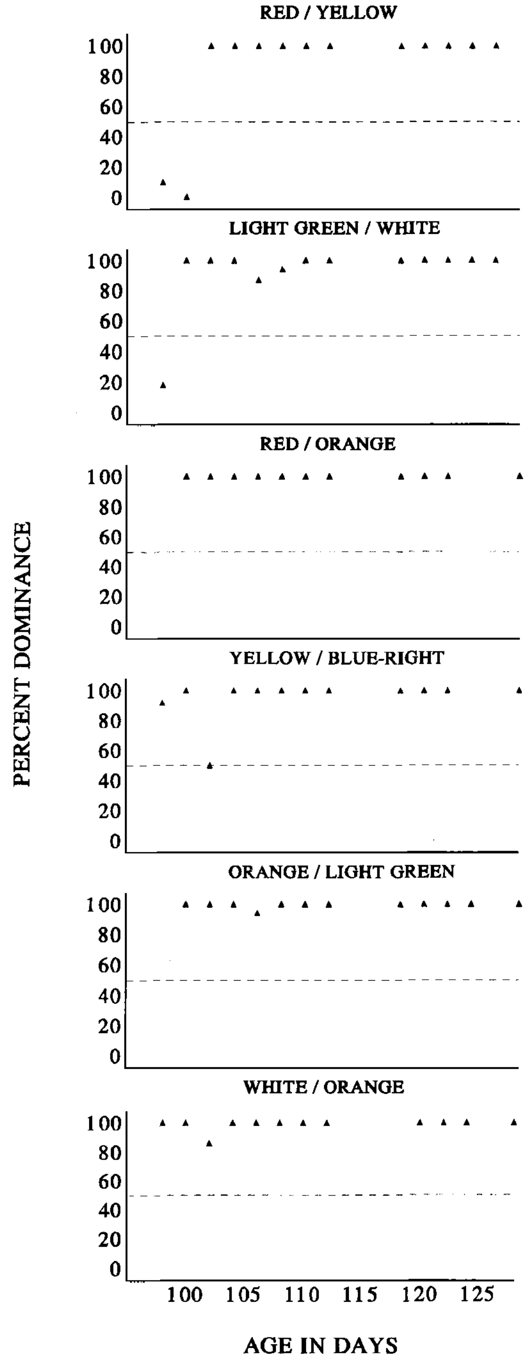

Fig. 2. Daily percentages of dominance interactions won (by individual listed first) in 6 of 15 dyads of hand-reared sparrows within the experimental flock. Data are shown for the least stable dyad (Red/Yellow), most stable dyad (Red/Orange), and four dyads of intermediate stability. Ages are not exact because hatching dates varied from 13 to 20 June. Dashed line indicates 50% dominance (equal number of interactions won by each member of dyad). In contrast to situation in earlier brood-mate flocks, sparrows established and maintained stable relationships after first four days of this experimental period.

and plastic song in the first nine months of life was similar to that reported in other passerines like Chaffinches (*Fringilla coelebs;* Nottebohm 1971) and Song Sparrows (*Melospiza melodia;* Nice 1943). Finally, social interactions of hand-reared sparrows with each other and with wild-caught birds were indistinguishable from each other and from interactions between wild-caught birds. The only perceptible difference between the behavior of hand-reared sparrows and that of the wild-caught birds was the remarkable tameness shown by the former group towards humans, dogs and cats. I conclude that, in spite of the unnatural conditions the hand-reared sparrows faced during the first seven months of their lives, they achieved a level of social development indistinguishable from that of wild-caught birds of similar age.

An unusual feature of the early agonistic behavior of the hand-reared sparrows was the preponderance of active pecks to the heads of opponents in the first day or so of exposure to other individuals. This behavior, which I have never observed in adults despite having witnessed more than 30,000 dominance interactions over four winters (see Piper and Wiley 1989, 1991), might be an artifact of the rearing conditions of the birds. Alternatively, early pecking might have resulted from the tendency of the young sparrows to approach each other closely, a possible indication that spacing behavior undergoes a developmental phase.

One of the most puzzling aspects of the agonistic behavior of young White-throated Sparrows was their tendency to engage in unstable dominance relationships between 46 and 100 days of age. Although they are not widely recognized, unstable periods of this kind occur in other passerines (e.g. Song Sparrows [Nice 1943], White-crowned Sparrows, *Z. leucophrys* [L. Baptista pers. comm.]) and apparently also in chickens (Rushen 1982).

The proximate cause of the unstable period is not immediately obvious. One possible cause is fluctuations in relative dominating abilities

TABLE 1. Dominance matrix for hand-reared sparrows in experimental flock. Birds ranked so as to minimize number of dominance interactions appearing under diagonal. Numbers in table indicate dominance interactions between 21 January and 17 March in which bird in column at left dominated bird in top row. For example, Red^1 dominated Blue-Right^4 62 times during this period, while Light Green^2 dominated Yellow^4 once. Superscripts indicate brood to which each bird belonged (1, 2, 3 or 4).

	Red^1	Orange^2	Yellow^4	Light Green^2	White^3	Blue-R^4
Red^1	X	77	62	114	2	62
Orange^2	—	X	41	85	1	34
Yellow^4	22[a]	5[a]	X	88	132	66
Light Green^2	2	1	1	X	150	66
White^3	124	83	4	14[a]	X	78
Blue-R^4	8[a]	—	2	1	16[a]	X

[a] Denotes that majority of these interactions, which were inconsistent with eventual dominance relationship in dyad, occurred in first four days that experimental flock was together. Exact numbers of "inconsistent interactions" occurring in first four days were: 22 of 22 for Yellow^4/Red^1 pair; 5 of 5 for Yellow^4/Orange^2; 9 of 14 for White^3/Light Green^2; 14 of 16 for Blue-Right^4/White^3; and 7 of 8 for Blue-Right^4/Red^1.

of sparrows over time: rapid fluctuations might cause reversals, while more gradual fluctuations might cause flip-flops. A prediction from this hypothesis is that an individual's success in dominance interactions against one opponent should be correlated with its success against others. This was not the case. Of 15 potential correlations between a bird's daily dominance percentages against one opponent and against a second opponent in the brood-mate flocks, none was significant (r-values ranged from -0.47 to 0.40; n-values from 21 to 33; P-values from 0.02 to 0.87; Bonferroni-adjusted maximum value for significance of many related statistical tests = 0.5/15 = 0.0033; see Rice 1989). A second possible explanation for the unstable period is that it resulted simply from a pronounced tendency of young sparrows to challenge dominant opponents. This hypothesis is consistent with the high frequencies of reversals and flip-flops during the unstable period and also would explain the decrease in frequency of energetically costly dominance interactions like fights and pursuits from the time of the brood-mate flocks through the final flock phase.

How might one explain the existence of an unstable period in evolutionary terms? If it is presumed that the unstable period occurs during the same interval in captive and wild sparrows, then it falls after fledging but at a time when the birds are still on the breeding ground. Although little is known about use of space and social behavior of juveniles during the post-fledging period (Falls and Kopachena 1994), one can surmise that juveniles passing through an unstable period would experience instability in dominance relationships with other juveniles and with adults they encountered. Although the instability might have a metabolic cost because it would result in frequent fights and other violent interactions with opponents (as seen in this study), it seems unlikely to have severe ecological consequences for the recently-fledged

TABLE 2. Dominance matrix for Final Flock 1. Mixtures of hand-reared isolates (indicated by "I"), hand-reared birds from experimental flock (denoted by "F"), and wild-caught birds (denoted by "W"). In all three final flocks (see also Tables 3 and 4), a hand-reared isolate assumed the top rank, wild-caught birds were ranked immediately behind, and remaining hand-reared sparrows (experimental flock birds and isolates) were lowest-ranking.[a]

	Blue-L^1-I	Black-Yellow-W	Green-Purple-W	Red-White-W	White^3-F	Orange^2-F	Purple^4-I
Blue-L^1-I	X	10	14	17	9	11	7
Black-Yellow-W	—	X	31	18	6	6	3
Green-Purple-W	—	—	X	6	2	5	7
Red-White-W	—	—	—	X	16	20	7
White^3-F	—	—	—	—	X	13	6
Orange^2-F	—	—	1	—	—	X	6
Purple^4-I	—	—	—	—	—	—	X

[a] Superscripts as in Table 1.

TABLE 3. Dominance matrix for Final Flock 2. Flock consisted of hand-reared isolates (denoted by "I"), hand-reared birds from the flock ("F"), and wild-caught birds ("W").[a]

	Light Blue^2-I	Blue-Yellow-W	Purple-Orange-W	Orange-Blue-W	Red^1-F	Dark Green^3-I	Yellow^4-F
Light Blue^2-I	X	16	21	8	—	24	27
Blue-Yellow-W	—	X	33	16	7	17	5
Purple-Orange-W	—	—	X	(19)[b]	(6)[b]	(17)[b]	(4)[b]
Orange-Blue-W	—	—	(8)[b]	X	17	11	3
Red^1-F	33	—	(5)[b]	—	X	18	17
Dark Green^3-I	1	—	(8)[b]	—	—	X	45
Yellow^4-F	—	—	(5)[b]	—	—	—	X

[a] Superscripts as in Table 1.

[b] Purple-Orange dominated Orange-Blue, Red^1, Dark Green^1 and Yellow^4, respectively, a total of 19, 6, 17 and 4 consecutive times from 21 January-9 March and, thus, established itself as third-ranking sparrow during this period. From 9-17 March, however, Purple-Orange was dominated by same four opponents in a total of 8, 5, 8 and 5 consecutive interactions, which indicated a sudden fall to seventh rank. This fall occurred in the absence of any observable change in condition or other behavior.

birds, which probably have access to abundant food at this time. However, it is difficult to imagine any selective advantage for the unstable period. Perhaps, like the sputtering subsong that occurs contemporaneously with it, the unstable period is a by-product of some aspect of social development occurring in young animals.

Like Arcese and Smith (1985), who studied determinants of dominance in Song Sparrows, I noted no correlation between dominance and either absolute nestling size or size of a nestling relative to its brood mates. Furthermore, I recorded only three isolated agonistic interactions among the sparrow nestlings in over 20 h of observation. Based on these findings, I conclude that the dominating abilities of adult sparrows are not strongly affected by events during the nestling phase. In contrast, dominance patterns in precocial birds seem strongly influenced by early dominance interactions with brood mates (Boag and Alway 1980).

Although the nestling phase did not appear to affect dominance in winter, the social environment experienced by White-throated Sparrows from four to seven months of age seemed to influence dominance strongly. The apparent effect might have resulted simply because of a general tendency for animals to be more aggressive than usual following a period of isolation (Cairns et al. 1985, Halperin and Dunham 1993). Unlike most studies of behavior following isolation, however, the subjects in the present study were not exposed to unnatural sensory deprivation, or to total isolation from conspecifics. In fact, isolates occasionally engaged in dominance interactions with sparrows housed in neighboring aviaries (either hand-reared or wild-caught birds), supplanting them or uttering brief notes of song when neither they nor their opponent across the wire mesh retreated immediately from a close approach. Thus, it is more difficult in the present study to attribute the behavior elicited by the isolation to gross deficiencies in sensory stimulation (Halperin and Dunham 1993).

Perhaps the increase in dominance among isolates resulted not from isolation per se, but rather from exclusive use of home ranges by

TABLE 4. Dominance matrix for Final Flock 3. Flock consisted of hand-reared isolates (denoted by "I"), hand-reared birds from the flock ("F"), and wild-caught birds ("W").[a]

	Black^4-I	Red-Green-W	Blue-Black-W	Light Green^2-F	Blue-R^4-F
Black^4-I	X	13	7	30	17
Red-Green-W	—	X	55	13	9
Blue-Black-W	—	—	X	18	5
Light Green^2-F	—	—	—	X	14
Blue-R^4-F	—	—	—	—	X

[a] Superscripts as in Table 1.

TABLE 5. Relationship between final dominance and: (1) treatment group (isolate, flock or wild-caught); (2) size, as indicated by wing chord. Although sample sizes were small ($n = 19$), treatment had a significant effect on final dominance and wing chord had a nearly significant effect.

Source of variation	Sum of squares	df	F-value	P
Treatment	0.553	2	4.211	0.035
Wing chord	0.265	1	4.034	0.063
Error	0.985	15		

the birds, an early form of territoriality that somehow improved the birds' abilities to dominate opponents in unfamiliar areas. Such an increase in dominating ability of isolates might have come about because they experienced no aggression from opponents for many weeks and thus became increasingly aggressive themselves. However, the three dominant isolates did not show an increased number of aggressive-type interactions in final flocks ($\bar{x} = 45 \pm 4\%$ incidence of attacks and pursuits among three dominant isolates, compared to 38 ± 18% among all others in final flocks; $t = 0.11$, $P > 0.5$; one-tailed t-test). Possibly the exclusive use of an area during the experimental phase led to a more subtle increase in a bird's "confidence" that was not easily measurable behaviorally. If exclusive use of home ranges did cause the apparent surge in dominating ability, this behavior pattern differs markedly from the development of site-dependent dominance, wherein a White-throated Sparrow rises in dominating ability within an area as it gains familiarity with that specific area (Dearborn and Wiley 1993).

The apparent correlation between early social environment and dominating ability in winter suggests the possibility of a critical period that influences dominating ability. If such a critical period exists, the development of dominance might parallel that of singing behavior (Kroodsma 1982), imprinting (Bateson 1976), and possibly site attachment (Ketterson and Nolan 1990), wherein the behavior of an adult animal is permanently influenced by events that occur during a relatively brief developmental period. Clearly, more research is needed to investigate the timing and strength of the effect of early social environment on dominance. Few studies of such developmental influences exist, in spite of some promising reports. For example, Arcese and Smith (1985) reported that early-hatched Song Sparrows achieved high rank regardless of their degree of association with home ranges, a result they regarded as potential evidence for an effect of social experience on dominance status. Westman (1990) found that dominance of young Great Tits (*Parus major*) was influenced by that of foster or genetic parents and the habitat in which they were reared. Finally, Rushen (1982) noted that early-maturing male chickens achieved high dominance rank.

The effect of early social environment on dominating ability in winter has important implications for the ecology and behavior of juvenile White-throated Sparrows. If a critical period for isolation occurs between the ages of four and seven months in free-living sparrows as in the captive birds I examined, a tendency for free-living birds to gain exclusive access to small areas between September and January of their first years of life might lead to high dominance rank in winter. A young sparrow might gain exclusive use of an area during this period by remaining on the breeding ground until late November or December (at which time most conspecifics would have moved south) or by residing in an area where conspecifics are scarce. Such behavior would require a young sparrow to suffer disadvantages (e.g. use of marginal habitat and possible death in event of harsh weather on breeding ground) in the short term that might lead to a great advantage (e.g. high dominating ability in winter). At present, too little is known about the behavior of first-year sparrows to determine whether some do maintain exclusive ranges and, thus, increase their ability to dominate others. Young White-throated Sparrows arrive on the wintering ground later than adults, on average (Piper and Wiley unpubl. data), a pattern that is consistent with the hypothesis of migratory delay by first-winter birds.

The apparent effect of early social environment on dominance is likely to be of substantial ecological importance in passerines generally. It already is clear that high dominance status can reduce predation risk (Schneider 1984, Piper 1990a), increase access to food (Alatalo and Moreno 1987), and increase long-term survivorship (Arcese and Smith 1985, Desrochers et al. 1988, Piper and Wiley 1990a). Hence, through their influence on dominating ability, early social conditions might be a major determinant of survivorship throughout life.

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