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Prior Residence Influences Contest Outcome in Flocks of Non-Breeding Birds

Emilie C. Snell-Rood & Daniel A. Cristol

Department of Biology, Institute for Integrative Bird Behavior Studies, College of William and Mary, Williamsburg, VA, USA

Abstract

We sought to determine whether early arrival was a determinant of contest outcome in loosely organized, non-breeding flocks of birds. In White-throated Sparrows (*Zonotrichia albicollis*) arrival date during autumn migration, i.e. within-year prior residence, was a significant determinant of contest outcome for those birds that were not present on the study site in previous years. To determine whether the advantage of early arrival was due to prior residence per se, as opposed to some correlate of arrival date (e.g. condition), we experimentally delayed the arrival of 60 migrants. We found a significant effect of the delay: the outcome of contests between naturally arriving (control) birds and experimentally delayed birds was significantly related to the difference between the control bird's natural arrival date and the experimental bird's delayed arrival date. Thus, prior residence per se, and not some correlate of arrival date, had a significant effect on a naïve individual's ability to win contests. Interestingly, arrival date had no effect on contest outcome among birds that had wintered on the site in previous years. Because a prior residence advantage accumulates in a time-dependent manner, our results suggest that fighting ability or perceived resource value increases with site familiarity. Thus, there may be selection on arrival date and site-faithfulness as behavioral strategies to increase access to resources.

Correspondence: Daniel A. Cristol, Department of Biology, Institute for Integrative Bird Behavior Studies, College of William and Mary, PO Box 8795, Williamsburg, VA 23187-8795, USA. E-mail: dacris@wm.edu

Introduction

Many species of birds join social groups during the non-breeding season to avoid predation (Powell 1974) and facilitate food-finding (Krebs et al. 1972). Contests over resources determine an individual's social rank within these groups and are major determinants of an individual's winter condition (Piper 1997). Although low-ranking individuals are generally in better condition within groups than alone (Ekman 1987; Hogstad 1989), their condition is often lower than that of high-ranking individuals. Higher-ranking birds have priority of access to clumped food and thus higher rates of energy intake (Piper 1990). Low-ranking birds are thus forced to take more risks (e.g. De Laet 1985; Lahti et al. 1997) and overall have a lower probability of survival than high-ranking individuals (e.g. Arcese & Smith 1985; Piper & Wiley 1990a).

Because the outcome of contests over food influences winter condition, and eventually fitness, it is important to understand the determinants of contest outcome. Past studies have focused on the role of an individual's age, size, and sex on contest outcome and social rank (e.g. Piper 1997). Although few of these characters are under individual control, one exception is prior residence. The asymmetry between contestants in the length of residence in an area often influences an individual's probability of winning a contest in territorial systems of many taxa (e.g. mammals, Haley 1994; insects, Kemp & Wiklund 2001). In birds, prior residence affects dominating ability in both territorial contests and contests within small, stable social groups (e.g. Eden 1987; Hogstad 1987; Nilsson & Smith 1988; Koivula et al. 1993). Prior residence also has significant effects on dominance in aviary tests in a variety of avian species (Yasukawa & Bick 1983; Cristol et al. 1990; Holberton et al. 1990; Wiley 1990; Sandell & Smith 1991). There is some evidence that the prior resident's advantage results from greater motivation (e.g. Krebs 1982), or, in some cases, inherently better fighting ability (e.g. Mönkkönen 1990). These asymmetries are often referred to as resource value or resource-holding potential, respectively.

Prior residence can have both a spatial and temporal component. Indeed, site-related dominance, whereby social rank is dependent on proximity to the center of the home range, can be an important determinant of status in birds with loosely organized flocks (Piper 1997). Prior residence also involves a temporal component, where a difference in arrival time between contestants plays a role in contest outcome.

The objective of this study was to better understand how prior residence affects contest outcome in free-living, loosely structured animal groups. Because arrival date in a new area varies with departure date and speed of travel, migratory or nomadic species (e.g. sparrows) may have a degree of control over their social rank in non-breeding season groups if a temporal component of prior residence plays a role in determining social rank. We studied two forms of temporal prior residence in a migratory bird: within-year prior residence (i.e. autumn arrival date) and between-year prior residence (i.e. whether or not present in a previous year), but focused our experimental effort on the former. First, we tested whether arrival date was a determinant of contest outcome in an unmanipulated flock of birds; then, at a nearby site we delayed the arrival of a subset of birds to determine if prior residence, rather than some correlate of arrival date (e.g. health), affected contest outcome. Our primary goal was to quantify the extent to which prior residence per se affects social rank.

Methods

Study Species and Site

We chose White-throated Sparrows (*Zonotrichia albicollis*), because their social structure typifies the loose social organization of many migratory species during the non-breeding season: large numbers of individuals interact over a large home range on which none of the birds will breed. They have previously been reported to exhibit a strong prior residence advantage that developed gradually for up to 2 wk in aviary cages (Dearborn & Wiley 1993). In addition, a spatial component of prior residence, site-related dominance (Piper 1997) has also been demonstrated in this species (Piper & Wiley 1989) and arrival date has been shown to be a correlate, albeit a weak one, of social rank (Piper & Wiley 1989). The White-throated Sparrow has been well-studied and several determinants of dominance in the non-breeding season are known (e.g. size, age, and proximity to familiar home range, Piper & Wiley 1989; Wagner & Gauthreaux 1990). This species occurs in two color morphs that differ in aggressiveness during the breeding season (Tuttle 2003), but we did not control for color morph as this variable has repeatedly been shown to have no effect on social status in winter (e.g. Piper & Wiley 1989; Dearborn & Wiley 1993).

Our two study sites were in a brushy woodlot on the campus of the College of William and Mary, Williamsburg, VA (37°15′39″N, 76°42′18″W). The area is bordered by mid-successional forest and a cemetery. This population has been banded each winter since 1997/1998 and in some winters almost 40% of the previous winter's residents return (D. A. Cristol, unpubl. data).

Effects of Arrival Date in an Unmanipulated Flock

We left the resident flock unmanipulated at one site and tested for the effects of arrival date on contest outcome while controlling for size (wing length) and previous-year experience. We captured all birds soon after arrival in the autumn, color-banded them for identification purposes, and then released them immediately to allow later observations of social interactions in the wintering flock.

Effects of Prior Residence in a Manipulated Flock

At a nearby site, we tested whether prior residence, rather than an unknown correlate of arrival date, had an effect on contest outcome, by experimentally delaying the arrival of a flock of birds and later observing their interactions with a control flock of birds upon release. The two sites (unmanipulated and manipulated) were 475 m apart. The linear range size of White-throated Sparrows is reported to average 85 m, with a maximum of 420 m (Piper & Wiley 1990b). Indeed, we detected very few birds moving between sites and treated them as independent studies.

The experimental flock was created by placing individuals in an aviary upon their first capture. The control flock was established by releasing individuals within 1 h after their first capture. Assignment of individuals to control or experimental flocks was random with the following constraints: to ensure that experimental and control flocks were of comparable composition, birds were matched across groups for arrival date (within 10 d), wing length (within 2 mm), previous-year experience, and minimum age. These pairings were not maintained for the analyses because some individuals were transients and left the site upon release. The experimental flock (n = 60 individuals) was released on Jan. 14, 2002; individuals within the flock had been held in captivity between 28 and 90 d, depending on their natural arrival date (range: 28–90 d, $\bar{x} \pm SD = 56.4 \pm 18.7$ d). Release was simultaneous to minimize the number of disruptions to the control flock. Upon release, the control and experimental flocks merged and individuals interacted at the food source. However, 11 members of the experimental flock were never resighted, probably because they had been transients still on migration when we placed them in captivity (24% of the new residents, 0% of the returning residents); thus 45 experimental birds were included in analyses of dyadic interactions. Among the 245 potential control birds captured and released, some also disappeared before resighting, presumably because they too had been transients that kept migrating (54% of the new residents, 14% of the returning residents). Because many new residents from each flock apparently continued their migrations before we included them in our data set, and the arrival dates and wing lengths of these probable transients did not differ significantly between flocks (D. A. Cristol, unpubl. data), we assume that the inclusion of some transients among our initial flocks did not bias our results.

Despite the fact that the experimental group was in captivity while the controls were free-living, we made a considerable effort to have experimental and control birds experience similar conditions. Birds were housed in an L-shaped outdoor enclosure [one rectangular portion 8.5 (length) × 2.4 (width) × 2.1 m (height), the other 2.9 × 7.2 × 2.1 m] with five conifer trees for roosting and five deciduous brush piles (0.8 × 1.2 × 1.6 m) for diurnal perching. A mixture of seed (cracked corn, white millet, turkey starter, sunflower chips, red millet, thistle, and grit, in a 4:3:3:2:1:1:0.25 ratio, respectively) was provided ad libitum in 12 dishes spread throughout the cage. The diet was supplemented with mealworms (*Tenebrio* sp.). Fresh vitamin/mineral-supplemented water was available ad libitum. Similarly, the diet of control birds in the field was supplemented with an identical food mixture available ad libitum (about 5 kg daily). Free-living birds were not provided with *Tenebrio* larvae, but had some access to wild invertebrates except during the coldest weather. Food-supplementation sites for the free-living birds resembled the set-up in the aviary, with similar brush piles and cut evergreen trees, all protected under 3 × 3 × 3 m wire-mesh enclosures that excluded predatory birds. Human-disturbance frequencies were comparable for both treatment flocks, as they were normally disturbed only once per day for feeding. The outdoor aviary and control site were 500 m apart, such that both sites experienced similar weather conditions. While flock sizes differed (delayed birds: n = 60; control birds: n > 100 at each site) density was likely similar in the foraging areas as 20–40 control birds were sometimes foraging in the same 5 × 5 m area. Thus, during social interactions and foraging, conditions were similar throughout the delay period for both experimental and control flocks.

Because the objective of this study was to quantify the effects of prior residence in birds that live in loosely organized flocks, pseudoreplication at the level of an individual within a flock was a necessary byproduct of our design. Pseudoreplication occurred in two instances. First, to delay the arrival of experimental individuals, we established a control and experimental flock (the former free-living, the latter in the aviary); thus, we had only one experimental and one control flock but regarded each individual as a separate replicate. Group-housing for the experimental flock was necessary because isolating captive birds in individual cages might have severely altered subsequent social behavior, and would have been less comparable to the situation of the free-living control birds. Because conditions during the delay were comparable between control and experimental birds, we believe it unlikely that there existed some factor other than the factor of interest, arrival date, that affected the rank of all birds in one group without also affecting the rank of individuals in the other.

Pseudoreplication also occurred in the analysis itself when considering dyadic interactions. Each unique pair of individuals contributed only a single datum. If more than one interaction was observed within a given dyad only one observation was included in the analysis; reversals were rare (<4.5%), and when they did occur those dyads were not included. However, several dyads had single individuals in common. We believe this problem is minimal because of the large sample size of dyads: among unmanipulated new residents, 103 individuals met in 141 dyads; for contests between returning residents, 47 individuals comprised 55 dyads, and among experimental-vs.-control new residents, 86 individuals comprised 84 dyads. To confirm that pseudoreplication was not responsible for our results, we repeated the analysis after eliminating all dyads but one for each individual.

Another concern about our design might be that the experimental birds formed relationships during captivity that carried over after release. We assumed that individual delayed birds were likely to behave independently of one another when the delayed and control flocks mingled after release, negating any significant coat-tail effects, in which the rank of a closely associated individual can bias the rank of another (Wiley 1990; Cristol 1995). This is probably of little concern here because White-throated Sparrows have very loose flocks (e.g. they associate more than expected by chance with only three to four birds out of over 100 flockmates, and spend only 20% of their time with these associates; E. C. Snell-Rood, unpubl. data). We did not even record the dominance relationships among delayed birds while they were in captivity because we were interested only in the eventual contests between released delayed birds and their free-living counterparts, so lingering relationships from the aviary should have had no effect on our results.

Estimation of Natural Arrival Date

Birds were likely caught soon after arrival because of the frequency and regularity of trapping and netting. Thus, we used an individual's first date of capture as an estimate of its arrival date. We captured individuals from Oct. 4 through Dec. 20, 2001 from dawn until at least 09:30 EST at two regularly baited sites (baiting began Sep. 25). Birds were captured with treadle traps (n = 15–20 at each site) and mist nets surrounding the trapping area (n = 4–5 at each site). We trapped birds on 53 d, averaging 5 d/wk. In addition, netting occurred once a week; on those days traps and nets were open until approx. 12:00 EST. As the intensity of migration increased (mid-Nov.) we opened half of the nets along with the traps on approximately three to four mornings per week.

Our estimates of arrival date were presumed to be accurate for several reasons. First, rates of capture did not vary with fluctuations in temperature (unpubl. data), indicating that we were not missing birds during periods of mild weather. Secondly, most birds were recaptured soon after their first capture, implying they were not averse to going in and out of traps: 82% of new residents captured more than once (n = 96) were recaptured within 11 d of their arrival date (for returning residents, 63% and n = 43). Of those birds captured only once (n = 116) 75% were caught during the last 10 d of trapping and thus did not have ample opportunity to be recaptured. Finally, when analyses were redone with only those individuals that were definitely not trap-shy (recaptured within 10 d), the results reported below did not change. Thus, birds were highly susceptible to trapping and our estimates of arrival date are accurate.

Contest Outcome

Following the release of the experimental flock (Jan. 14, 2002), the senior author gathered all data on dominance interactions while unaware of which birds were in each treatment group. For the unmanipulated flock, observations occurred on 14 d (1567 total min) from Jan. 16 through Mar. 25, 2002. For the manipulated flock, observations took place on 13 d (1762 total min) between Jan. 20 and Mar. 29. When < 10 individuals were present at the site, all dominance interactions were recorded with a Dictaphone. When > 10 individuals were present, focal individuals were chosen quasi-randomly in a way that avoided bias due to rank or activity level, and all of their interactions recorded until they went out of view. We observed 737 interactions within the unmanipulated flock and 706 at the other site. In dyads with multiple interactions, we observed very few reversals (< 5%). Thus, a single interaction was indicative of the dominance relationship in a dyad, as previously reported for this species (Piper & Wiley 1989).

Because the flocks were so large (> 200 individuals each), we do not report traditional measures of social rank that assume a linear dominance hierarchy (although results for such an analysis are entirely comparable to the ones presented here). Instead, we used logistic regression to analyze the factors that influence an individual's probability of winning any given interaction.

Morphological Measurements

For size estimation we measured the wing chord (unflattened) of each individual twice to the nearest 0.5 mm, and the tarsus length three times to the nearest 0.1 mm with digital calipers. Sex and size are correlated in White-throated Sparrows, such that 89.5% of females have wing lengths of <70 mm and 91.9% of males have lengths >70 mm (Piper & Wiley 1991). We drew blood from all intermediate-size individuals ($n = 120$, wing >68 and <74.5) to determine sex. Mass and fat were measured at approximately the same time on the morning of capture and the morning of release. Fat was estimated visually from subcutaneous deposits in the furcular cavity on a scale of 0–5 where almost all birds received a 1 ($<$one-third full), 2 ($<$two-thirds full), or 3 (nearly level). Minimum age was assessed by a combination of capture/sighting data from previous years and skull ossification. Finally, each individual was fitted with a metal band and three color bands in a unique combination. To be cautious, we did not use yellow or white bands, colors that appear prominently in the head of this species, even though color bands have been shown to have no effect on dominance in White-throated Sparrows (Piper & Wiley 1989; Johnson 1999).

Molecular Sex Determination

We used the methods of Griffiths et al. (1996, 1998) to sex intermediate-size birds. Blood samples (15 μl from brachial vein) were stored in 1 ml Queen's lysis buffer (Seutin et al. 1991) at 4°C until extraction. DNA was extracted using a 5 M salt solution (Miller et al. 1988). A 25 μl PCR reaction was run for each sample with final reaction conditions of 1.5 mM $MgCl_2$/Taq buffer, 200 mM of each dNTP, 200 ng of each primer (P2 and P8, see Griffiths et al. 1996, 1998), 0.5 U Taq polymerase (Eppendorf HotMaster, Eppendorf North America, Westbury, NY, USA), and 50–200 ng genomic DNA. The PCR thermal cycling program was as follows: initial denaturing for 2 min at 94°C, followed by 30 cycles at 94°C for 30 s, 50°C for 45 s, and 70°C for 30 s, concluding with final steps at 48°C for 1 min, and 72°C for 5 min. Reaction products were electrophoresed for 2 h at 70 V in a 2% NuSeive 3:1 agarose gel stained with ethidium bromide. Two bands indicated a female; one band indicated a male. Ten percent of DNA samples were tested twice to confirm accuracy and 100% of these were consistent with initial results.

Statistical Analyses

JMP 3.1 (SAS Institute, Cary, NC, USA, 1995) was used for all analyses. We conducted preliminary analyses on the effects of different independent variables on social rank to determine which confounding factors should be included in the final analysis. Our various measure of size were correlated with one another. Age and previous-year experience on the site were also closely related. Finally, sex and size are correlated in White-throated Sparrows (Piper & Wiley 1991), and both may have effects on social status (Piper & Wiley 1989; Wagner & Gauthreaux 1990). In the preliminary analysis, correlated factors were entered into a general linear model for the social rank of an individual (the proportion of contests won). Of the correlated size measurements, wing length was the only significant determinant of rank (wing length $F_{3,85} = 11.8$, $p = 0.0009$; tarsus length $F_{3,85} = 0.43$, $p = 0.51$; mass: $F_{3,85} = 0.01$, $p = 0.91$). Wing length and sex were correlated, but wing length was a significant predictor of social rank ($F_{2,23} = 4.51$, $p = 0.045$), while sex was not ($F_{2,23} = 1.51$, $p = 0.23$). Previous-year experience had a detectable effect on rank ($F_{5,61} = 18.37$, $p < 0.0001$), while its correlate, age, did not ($F_{5,61} = 1.47$, $p = 0.22$).

For our analysis we used logistic regression to identify the determinants of contest outcome at the unmanipulated and manipulated sites. Given the results of the preliminary analysis, we controlled for differences in prior-year experience by analyzing contests between new and returning residents separately. Wing length was included in the model, but sex and age were not.

Results

Was Arrival Date a Determinant of Contest Outcome Between Controls?

For individuals without previous-year experience, earlier arrival date and longer wing length relative to the opponent increased the probability that an individual would win a particular contest (Fig. 1, Table 1). When the analysis was repeated without including any individuals more than once, arrival date had an

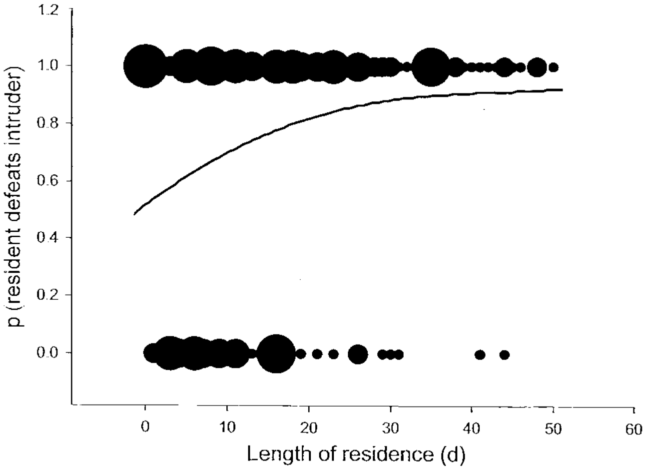

Fig. 1: Outcome of contests between unmanipulated individuals without previous-year experience. Individual contests are shown with filled circles; contests won by the early arriving individual are at Y = 1 and those won by the late-arriving individual at Y = 0. The line is the solution to the logistic regression and controls for wing length asymmetry between contestants. The number of days the early arriving individual in a pair arrived before their opponent had a significant positive effect on the probability of winning a contest. Circle size corresponds to number of dyads

Table 1: Logistic regression for contests among unmanipulated new or returning residents

	New residents	Returning residents
Overall model	$n = 141, R^2 = 0.10$, $\chi^2 = 16.47, p < 0.001$	$n = 55, R^2 = 0.07$, $\chi^2 = 5.52$, ns
Arrival date	Wald $\chi^2 = 7.99, p < 0.01$	Wald $\chi^2 = 0.15$, ns
Wing length	Wald $\chi^2 = 5.82, p < 0.05$	Wald $\chi^2 = 4.86, p < 0.05$

effect while wing length did not (overall model $n = 41$ dyads, $R^2 = 0.18$, $\chi^2 = 9.91$, $p = 0.02$; arrival date asymmetry: Wald $\chi^2 = 5.36$, $p = 0.02$, wing length: Wald $\chi^2 = 0.12$, $p = 0.75$). However, for birds returning from a previous year, an asymmetry in arrival date between contestants did not predict contest outcome (Table 1), although power for this test was much lower than for contests among individuals without previous-year experience. Thus, unmanipulated arrival date was correlated with contest outcome, but only for birds without previous-year experience.

Does Prior Residence Per Se Have an Effect on Social Status?

We predicted that delayed birds would have a decreased probability of winning contests against earlier-arriving control birds when we controlled for size. For contests among experimental and control birds without previous-year experience, the length of the control bird's residence (i.e. the length of time between the control bird's arrival and the experimental bird's release) was

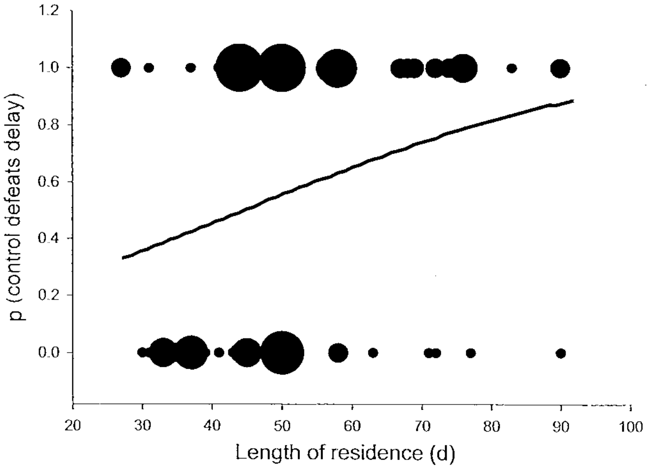

Fig. 2: Outcome of contests between naturally arriving control individuals and delayed individuals. Individual contests are shown with filled circles; contests won by the controls are at $Y = 1$ and those won by the experimentally delayed individual are at $Y = 0$. The line is the solution to the logistic regression and controls for wing length asymmetry between contestants. The number of days the control individual in a pair arrived before the delayed release of its experimental opponent had a significant positive effect on the probability of winning a contest. Circle size corresponds to number of dyads

significant in determining contest outcome, while wing length asymmetries were not (overall model: $n = 86$, $R^2 = 0.11$, $\chi^2 = 13.50$, $p < 0.01$; arrival date: Wald $\chi^2 = 5.84$, $p < 0.05$; wing length: Wald $\chi^2 = 2.09$, $p < 0.15$; Fig. 2). This effect remained as a trend when the analysis was repeated on the smaller sample of dyads that did not contain the same individuals ($n = 19$, $R^2 = 0.12$, $\chi^2 = 0.03$, $p = 0.08$). Sample size was too low ($n = 20$ dyads) to analyze contests between control and delayed returning residents. This response of contest outcome to an experimental manipulation of arrival date indicates that prior residence per se, rather than a correlate of arrival date, affected social rank.

Effects of Captivity

One could argue that the decreased probability of winning contests that we observed for delayed birds was an artifact of their captivity instead of the effects of late arrival on the site. Several lines of evidence suggest that this is unlikely. First, duration of captivity did not have significant effects on outcome of contests when controlling for wing length and residence asymmetries (overall model: $n = 86$, $R^2 = 0.12$, $\chi^2 = 14.05$, $p < 0.01$; wing length: Wald $\chi^2 = 2.25$, ns, residence asymmetry: Wald $\chi^2 = 5.96$, $p < 0.05$, duration of captivity: Wald $\chi^2 = 0.57$, ns). Secondly, the delayed birds appeared to be in good condition. All 60 survived the 1–3 mo period in the aviary and all but three individuals gained weight and fat before release. Average weight gain was 2.4 ± 2.1 g and increase in fat score was 1.4 ± 1.1 units, which was similar to the changes recorded for 125 individuals sampled in the field during this time period (mass: $\bar{x} = 2.2 \pm 1.6$ g, fat: $= 1.5 \pm 1.0$ fat units, $n = 125$).

Discussion

Does Prior Residence Affect Contest Outcome in Loosely Organized Flocks?

We found that a White-throated Sparrow's autumn arrival date played a significant role in contest outcome in loosely structured winter flocks for birds that had not established residency in previous years. For instance, an individual that arrived only 15 d prior to a size-matched opponent had an 80% chance of defeating that opponent in any given contest (Fig. 1). Such arrival asymmetries are biologically relevant as new residents arrived over a 4-mo time span (Oct. through Jan.). To distinguish between the effects of prior residency per se and the possible effects of any correlates of arrival date, we delayed the arrival of a flock of birds at an independent site, predicting that the delayed arrival date of the experimental birds, but not their natural arrival date, would determine contest outcome. As predicted, delayed birds were at a disadvantage in contests against control birds, and the prior residence advantage was dependent on the number of days between the natural arrival of the control and the experimental arrival (i.e. release date) of the delayed bird (Fig. 2). The delay affected social status in a time-dependent manner. It is unlikely that the negative effects of the delay were due to some artifact of captivity because the length of time in captivity played no role in the outcome of contests. Thus, our results indicate that prior residence per se, in the form of autumn arrival date in a migratory bird, is a significant determinant of contest outcome in the non-breeding season, but only for first-time residents.

We have demonstrated that within-year prior residence (i.e. fall arrival date) is important for newcomers to a site. Previous-year experience is also a potent determinant of dominance in these birds. But why did returning residents not gain an additional advantage from early arrival? Methodology problems, such as low power (Table 1) or inaccurate arrival date estimates for experienced birds could potentially explain this difference. Alternatively, returning birds might remember previous dominance relationships which would then be unaffected by relative arrival dates (Wiley et al. 1999). Returning birds may also remember essential characteristics of the site that boost fighting ability, such as food patches and escape routes, so that no additional advantage is gained by familiarization through earlier arrival.

Why does Prior Residence Affect Social Status?

Traits can influence dominating ability because they are correlated with fighting ability, an individual's motivation, or an arbitrary rule adopted by a population (Maynard Smith & Parker 1976). Our results support previous work suggesting that prior residence is not due to an arbitrary rule 'yield to resident' (Grafen 1987; Stutt & Willmer 1998) because the residence advantage builds over time. Likewise, our results eliminate the possibility that a prior residence advantage may be due to a correlation between fighting ability and natural arrival date (e.g. Potti 1998), because delayed individuals that had originally arrived early lost their contests with later-arriving, but non-delayed, individuals. Analogous experiments in other systems have yielded similar results (e.g. Sandell & Smith 1991; Koivula et al. 1993).

This and other studies (field tests: Beletsky & Orians 1989; Tobias 1997; laboratory tests: Krebs 1982; Figler & Einhorn 1983; Dearborn & Wiley 1993) show that a prior residence advantage is a function of time. This suggests that the mechanism of prior residence may be an increase in an individual's motivation to fight as their familiarity with a site and the resource value increases (e.g. Krebs 1982). Familiarity with a site may also increase an individual's condition. To the extent that condition is related to fighting ability, this familiarity may thus increase an individual's resource-holding potential, independent of motivation. For example, familiarity with local food conditions (e.g. patch distribution, average patch quality) would allow individuals to find food more quickly (e.g. Kirk & Houston 1995). In addition, experience with handling local food increases foraging efficiency (e.g. Goss-Custard et al. 1998). Finally, familiarity with conspecifics may decrease levels of aggression and allows more efficient foraging within flocks. Thus, residents likely gain an advantage in contests with late-arriving birds because they have a greater fighting ability.

This hypothesis of an increase in fighting ability with familiarity is parsimonious with respect to our observations of the prior residence effects accrued through both within- or between-year prior residence. Early arriving individuals gain familiarity with the site that improves their condition relative to late-arriving individuals in the same year. Individuals returning from previous years retain familiarity that allows an increase in condition relative to simultaneously arriving individuals without previous-year experience. The mechanism for each of these types of prior residence is still unknown and of great interest in systems where social status impacts fitness.

Prior Residence as a Behavioral Strategy

Social rank and contest outcome are significant determinants of winter condition and survival in relation to both access to resources and probability of predation (e.g. Arcese & Smith 1985; De Laet 1985; Lahti et al. 1997). Indeed, in this population of White-throated Sparrows, social rank is positively related to nutritional condition, as indicated by a correlation between rate of feather regrowth and degree of despotism in captive flocks (Jenkins et al. 2001).

Our results indicate that early arrival date may confer some intrinsic fitness benefits by increasing a bird's success at winning contests, possibly through time-dependent increases in fighting ability. Thus, as opposed to many of the fixed determinants of dominance such as sex and size (reviewed in Piper 1997), selection could potentially act on variation in arrival time as a mechanism of individual context-dependent strategies. For instance, selection may lead to mechanisms for early or rapid migration by individuals settling in an area for the first time. This would include all young animals, and older animals in species which shift to new wintering areas as they age, such as many birds with differential migration (Cristol et al. 1999). Individuals that expect to winter in the same location as previous years might increase their fitness more by staying longer on the breeding grounds to stake a claim to future breeding territories. In addition, annual variation in the severity of conditions at breeding or wintering sites may lead to variance in optimal arrival time: a lower rank may be more tolerable in a mild winter, selecting for later arrival date. Clearly, because of the tradeoffs involved in breeding site departure and wintering site arrival, and the dependence of an individual's priority of residence on the arrival dates of all other members of the population, this is a behavioral ecology problem ripe for modeling.

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