Prior residence has a gradual influence on dominance in captive white-throated sparrows

DONALD C. DEARBORN* & R. HAVEN WILEY

Department of Biology, University of North Carolina, Chapel Hill, NC 27599-3280, U.S.A.

Abstract. To investigate the influence of prior residence on dominance in captive white-throated sparrows, *Zonotrichia albicollis*, 28 groups of six birds each were studied in outdoor aviaries during winter. After periods of prior residence ranging from 2 to 45 days, the three highest-ranking birds in each of two aviaries were placed together in one of the aviaries and the three lowest-ranking birds from each aviary were placed together in the other aviary. The influence of prior residence increased gradually over at least 2 weeks to an asymptote at which individuals with the advantage of prior residence dominated newcomers in approximately 90% of the cases. In the initial groupings of unfamiliar birds, when only intrinsic features of individuals influenced dominance, only size (as indicated by wing length) correlated with dominance. The gradual increase in dominance of residents over newcomers suggests that prior residence is not used for conventional settlement of disputes. This influence of prior residence on dominance provides a mechanism for the tendency of an individual white-throated sparrow in the field to dominate more opponents at the centre of its range than at the edge.

Among wintering white-throated sparrows, *Zonotrichia albicollis*, an individual's success in dominating opponents can affect its access to food and shelter, its ability to store fat, and its probability of survival (Schneider 1984; Piper 1990a, b; Piper & Wiley 1990a, b; Wiley 1991). An individual's dominance in turn depends on intrinsic attributes, such as its age, sex and previous experience with dominance (Piper & Wiley 1989a, 1991a; Archawaranon et al. 1991). In addition, recent study has shown that a bird's dominance decreases with distance from the centre of its range (Piper & Wiley 1989a).

This variation in dominance with location could develop if individuals used their ranges unevenly and the duration of prior residence in a place increased the chances of dominating newcomers there. An influence of prior residence has been documented in captive groups of dark-eyed juncos, *Junco hyemalis*, a related emberizine, in which birds with prior experience in an aviary tend to dominate later additions (Balph 1979; Yasukawa & Bick 1983; Cristol et al. 1990; Holberton et al. 1990; Wiley 1990). In studies of a variety of other species, the interactions of residents and intruders also

suggest an influence of prior residence on dominance (Brown 1963; Phillips 1971; Zayan 1975; Davies 1978; Reichert 1978; Hyatt & Salmon 1978; Wiley & Wiley 1980; Krebs 1982; but see Arcese & Smith 1985; McVey 1988). However, no experimental studies of the influence of prior residence on dominance have been conducted with a species for which field studies have shown that dominance varies with location.

The mechanisms by which residence influences dominance also need attention. Prior residence might confer an advantage in contests for two fundamentally different reasons. First, residence in an area might increase an individual's familiarity with resources and shelter (Metzgar 1967; Ambrose 1972; Zach & Falls 1976; Davies & Houston 1981; Isbell et al. 1990), so that availability of resources for a resident would increase and risks decrease over time. The value of an area for a resident might thus eventually become greater than the value of other intrinsically similar areas. Consequently, an asymmetry of payoffs in contests between a resident and a newcomer would increase with time. Furthermore, as a consequence of greater access to food, residents might have more nutrients or energy available and thus have greater fighting capabilities than intruders. For either of these reasons, it would pay for a resident to invest more in contests than

*Present address: Division of Biological Sciences, University of Missouri, Columbia, MO 65211, U.S.A.

a newcomer (Maynard Smith & Parker 1976; Hammerstein & Parker 1982).

Second, prior residence might serve as an arbitrary asymmetry for conventional settlement of contests. This condition is evolutionarily stable only if all individuals are approximately (but not necessarily exactly) equal in their chances to be either resident or newcomer, in their payoffs from winning or losing, and in their capabilities for fighting (Maynard Smith 1974; Maynard Smith & Parker 1976; Davies 1978; Hammerstein 1981; Franke Stevens 1988). This possibility does not require a gradual development of familiarity with a location; instead, any advantage of a conventional settlement on the basis of prior residence would accrue as soon as two opponents differed in their occupation of an area.

The simplicity of finding food or shelter in aviaries reduces any direct advantages of familiarity with an area on availability of resources, as required by the first mechanism. Nevertheless, birds might have evolved adaptations for increasing their commitments in contests over a period of time that would, in natural circumstances, normally allow the development of advantages in foraging or seeking shelter. If this mechanism operates in captivity, one would expect a relatively slowly developing influence of prior residence on dominance. The second mechanism for advantages of prior residence, as a result of conventional settlement for contests, should in contrast produce clear effects of prior residence after short periods of time.

The present experiments examined these hypotheses for white-throated sparrows by determining the time required for an effect of prior residence to develop in captive birds. Even though an individual's location within its range is the strongest influence on its dominance in the field (Piper & Wiley 1989a), nothing is known about the time required for this effect to develop.

In addition, these experiments provided an opportunity to investigate intrinsic influences on dominance in initial groupings of captive birds. Dominance relationships in random groupings of unfamiliar opponents in unfamiliar locations are not affected by any situational differences among individuals. Previous studies of captive white-throated sparrows have suggested that sex, age and size, as indicated by wing length, influence dominance in initial groupings. There are conflicting reports concerning the influence of crown coloration or genetic morph on dominance in

captivity (Watt et al. 1984; Schlinger 1987; Schwabl et al. 1988).

METHODS

Wintering white-throated sparrows were studied in captivity at Mason Farm Biological Reserve, Chapel Hill, North Carolina, during the winters of 1988–1989 and 1989–1990. The basic design was to place groups of six birds in each of two aviaries for pre-determined periods of time and then to rearrange the birds in the two aviaries, by placing the three highest-ranking birds from each aviary in one of the aviaries and the three lowest-ranking birds from each aviary in the other. In 1988–1989 and 1989–1990, we studied birds in six and eight pairs of aviaries, respectively (28 aviaries in all).

Birds were caught at 17 locations at 25-m intervals along a hedgerow. We examined each bird to determine its degree of skull pneumatization, its wing chord, and the coloration of its crown stripes (Piper & Wiley 1989b). Each bird was individually marked with coloured bands. Groups of six birds were then placed in nearly identical outdoor aviaries measuring $2 \times 2 \times 2$ m. The birds in any one group had been trapped at least 50 m apart, far enough to assure little overlap in their ranges (median diameter of ranges in this population: 66 m; Piper & Wiley 1990b).

In order to reduce intrinsic influences on dominance within groups both before and after the exchanges of birds between pairs of aviaries, we initially grouped birds in each pair of aviaries by either sex or age, two correlates of dominance in a field study of this population (Piper & Wiley 1989a). In 1988–1989, we grouped birds by age, either first winter or older as indicated by cranial pneumatization (Wiley & Piper 1992). In 1989–1990, we grouped birds into two classes by wing chord ($\leqslant$ or > 70 mm) to maximize the separation of sexes. This procedure correctly assigned the sex class of 89·5% of females and 91·9% of males in this population (Piper & Wiley 1991b). Captive birds were supplied with unlimited food. Three of the 168 birds died of unknown causes in the course of the experiments, and one other bird was removed because of accidental injuries. Each aviary had four food dishes, a water dispenser, perches and shelter in standardized locations.

Behavioural observations were undertaken in the morning, usually between 0730 and 1030 hours from an observation chamber with a window of one-way

glass. To stimulate interactions, birds were deprived of food for 30–75 min, then provided with one dish of seed in the centre of the aviary. Most interactions occurred at or near this dish; encounters elsewhere in the aviary invariably followed the same patterns as those near the food. Interactions between birds fit one of four categories: (1) supplantations, in which one bird approached the dish and replaced another; (2) attacks, similar to supplantations but involving a rapid approach to the feeding bird; (3) hold-offs, in which the feeding bird did not move in response to another bird's approach; and (4) actual fights between two individuals. The last interaction occurred very infrequently (three of 4993 interactions). Individuals' relationships were consistent for all four types of interactions. One individual was considered dominant over another if it won at least 75% of the interactions for that dyad (Piper & Wiley 1989a). Because the first interaction between two birds in our study predicted their final dominance relationship in 96·8% of cases ($N = 662$ dyads meeting the 75% criterion based on two or more interactions), we considered one interaction sufficient to characterize dominance. Dominance ranks in each aviary were determined from dominance–subordination matrices arranged to minimize interactions below the principal diagonal. Prior to rearranging birds between aviaries, we observed a mean of 70·7 interactions per aviary (range = 26–208; $N = 28$); following rearrangement, we observed a mean of 119·4 (range = 17–364; $N = 26$). As a result of low rates of interaction during warm weather, we obtained too few observations to determine a dominance hierarchy in one pair of aviaries following rearrangement.

The period of prior residence, during which the groups of birds occupied their original aviaries, ranged in length from 3 to 45 days. After this period, the three highest-ranking birds from each of two aviaries were placed together in one of the aviaries and the three lowest-ranking birds from these two aviaries were placed together in the other. Thus each new group contained three residents and three newcomers, all with similar dominance ranks in their original aviaries. To standardize effects of handling, all individuals were caught and held in bags for 5–10 min and then released simultaneously. Prior residence in the aviary was thus the only systematic difference among them.

Birds combined in new groups by these exchanges had been in captivity in their original aviaries for the same periods of time, with one exception. In the exceptional case, there was a 3-day difference in time before the first switch after a period of prior residence greater than 30 days, so the proportional difference in time before this exchange was relatively small.

For the six birds in each aviary following an exchange, there were nine possible dyadic combinations of the three residents with the three newcomers. For a few aviaries, one or two of these combinations contributed no information about effects of prior residence as a result of tied dyads or insufficient data. To analyse the effects of prior residence, we calculated the proportion of resident–newcomer dyads in which the resident was dominant (called henceforth the prior residence proportion), so each aviary contributed one observation for statistical analysis. If all such dyads conformed to an effect of prior residence, the prior residence proportion would equal 1·0; if dyads were determined at random, the prior residence proportion would on average equal 0·5.

To determine correlates of dominance in the initial groupings, we assigned each bird a dominance score equal to the proportion of its known dyadic relationships in which it was dominant. This score was then used as the dependent (criterion) variable in linear models (Wilkinson 1988) with the following independent (predictor) variables: length of wing chord, coloration of crown stripes, morph, cranial pneumatization (incomplete or complete), and sex. Because the last three variables were categorical and the first two continuous, these linear models constituted an analysis of covariance. After November only incompletely pneumatized birds could be aged with certainty, because the skulls of some first-winter individuals began to reach full development at this time (Wiley & Piper 1992). Thus, we also included season (before or after 1 December) as an independent categorical variable in the models. Preliminary analyses revealed that no interaction terms among the independent variables approached significance, so they were excluded from the final analyses, with one exception. The interaction between age and season was retained to control for the seasonal change in our ability to determine age.

Morph was determined with an overall accuracy of 89% from a formula that combined information on coloration of the median and lateral crown stripes, age as indicated by cranial pneumatization, and sex as indicated by wing length (Piper & Wiley 1989b).
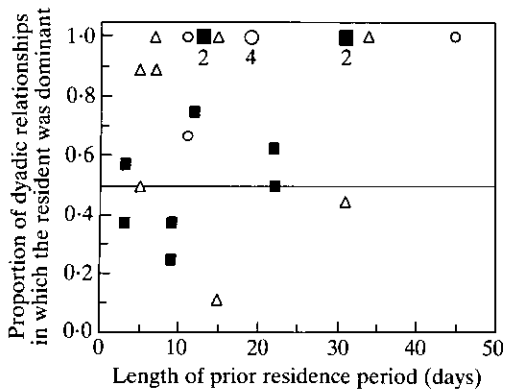
Figure 1. Proportions of dyadic relationships fitting an effect of prior residence in 26 aviaries following rearrangements of individuals after various periods of time. ■: Groups of mixed sexes (not sorted by wing length); △: groups composed predominantly of males (long wing lengths, > 70 mm); ○: groups composed predominantly of females (short wing lengths, ≤ 70 mm). Numbers below symbols indicate numbers of aviaries with the same results.
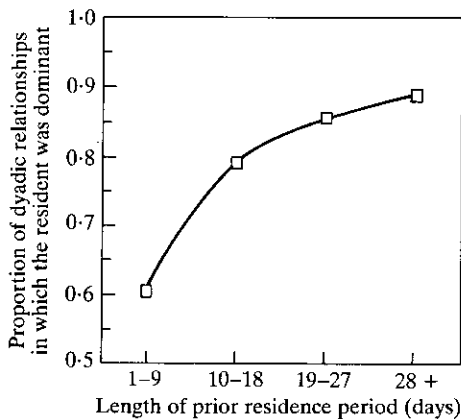

Figure 2. Proportions of dyadic relationships fitting an effect of prior residence following rearrangements of birds after various periods of time, grouped in blocks of 9 days.

RESULTS

The majority of the groups, before and after re-arrangements of birds, had strictly linear hierarchies (38 of 55). The frequency of groups with intransitive relationships was nevertheless higher (17 of 55) than previously reported for dark-eyed juncos in similar situations (Wiley 1990). Once a group of birds had become established in an aviary, its hierarchy was invariably stable.

Table I. Influences on dominance among first-winter birds in the initial aviaries (analysis of covariance, $N = 33$ individuals in six groups, $r^2 = 0.256$)

Variable	df	Mean square	F	P
Wing length	1	0.672	8.70	<0.01
Morph	1	0.024	0.31	NS
Error	30	0.077		

Table II. Influences on dominance among birds with short wings (predominantly females) in the initial aviaries (analysis of covariance, $N = 45$ individuals in eight groups, $r^2 = 0.130$)

Variable	df	Mean square	F	P
Wing length	1	0.213	2.15	NS
Morph	1	0.163	1.65	NS
Age	1	0.021	0.21	NS
Season	1	0.058	0.58	NS
Age* season	1	0.008	0.083	NS
Error	39	0.099		

*Interaction.

Table III. Influences on dominance among birds with long wings (predominantly males) in the initial aviaries (analysis of covariance, $N = 46$ individuals in eight groups, $r^2 = 0.075$)

Variable	df	Mean square	F	P
Wing length	1	0.038	0.34	NS
Morph	1	0.189	1.71	NS
Age	1	0.134	1.21	NS
Season	1	0.013	0.12	NS
Age* season	1	0.004	0.04	NS
Error	40	0.111		

*Interaction.

Following rearrangements of individuals and excluding the two aviaries for which we observed too few interactions for analysis, we had 26 aviaries for which we could calculate prior residence

proportions. The results clearly demonstrated an effect of prior residence, as most groups had prior residence proportions greater than 0·5 (binomial test, $N=24$ aviaries with prior residence proportions different from the random value of 0·5, one-tailed $P=0·003$, based on previous predictions that deviations from random, if any, should be in the direction of an effect of prior residence). Nevertheless, there was considerable variation among groups in prior residence proportions (Fig. 1).

The changes in prior residence proportions across 9-day blocks of prior residence suggested that the average effect of prior residence increased rapidly and then approached an asymptote after about 30 days, when at least 90% of dyadic interactions fit predictions for an influence of prior residence (Fig. 2). Comparison of the 1988–1989 and 1989–1990 data indicated that there was no difference in the proportions of male, female, or mixed aviaries to display an effect of prior residence ($\chi^2=1·44$, $df=2$, $P>0·4$; based on a contingency table for the distribution of prior residence proportions greater or less than 0·5).

The only independent variable associated with dominance in the initial groupings was length of wing chord, and this association appeared only in groups sorted by age. In six groups of birds in their first winter (cranial pneumatization incomplete), dominance was significantly related to wing chord but not to morph ($r^2=0·256$, Table I). Separate analysis with coloration of crown stripes rather than morph as an independent variable yielded similar results with a slightly lower proportion of variance explained ($r^2=0·249$). In two groups of birds with complete cranial pneumatization, dominance was again significantly related to wing chord ($F_{1,10}=10·52$, $N=12$, $P<0·01$); measurements of the crown stripes were not obtained for these birds.

In groups sorted to separate the sexes, dominance was not associated with wing chord, morph, cranial pneumatization or season (Tables II and III). Thus, within each sex, wing length had no significant association with dominance. The lack of any significant interaction between age and season showed that the absence of a significant influence of age on dominance held just as well for birds captured before December, when nearly all hatching-year birds can be identified by incomplete pneumatization of the skull, as for those captured later.

DISCUSSION

Gradual Development of an Influence of Prior Residence

In these experiments, the effect of prior residence was never absolute, even after extended periods of prior residence. The causes of this variation are not clear, but one possibility is that intrinsic differences between birds outweighed an effect of prior residence in some dyads. Although we grouped birds by age or sex in order to reduce such intrinsic differences, our analysis of the correlates of dominance in the initial groupings indicated that we had not eliminated the effects of all intrinsic differences in any of our cases.

Nevertheless, it is clear that prior residence has a pronounced influence on dominance in captive white-throated sparrows. This demonstration complements the finding that location influences dominance in the field (Piper & Wiley 1989a). We can conclude that birds have higher dominance proportions near the centres of their ranges in the field at least in part because dominance over newcomers increases with the duration of prior residence in a location.

In natural circumstances, individuals tend to stay in locations where they are dominant. Studies of white-throated sparrows in the field have shown that high-ranking individuals tend to have smaller ranges than low-ranking birds and that they tend to stay within their ranges even when the availability of food is reduced (Piper & Wiley 1989a, 1990b; Piper 1990b). Thus, dominance in a particular location leads to residence there, just as residence in a particular location leads to dominance. These reciprocal influences generate the wide behavioural spectrum observed in a natural population, from individuals that develop high rank within restricted ranges to those that remain low in rank throughout large areas.

In our experiments an advantage in dominance appeared in some cases after prior residence in an aviary for 1 week or less. The development of an effect of prior residence within days agreed with the finding that young dark-eyed juncos, usually subordinate to adults, could achieve dominance after only 1 week of prior residence in captivity (Cristol et al. 1990). Nevertheless, on average, the effects of prior residence continued to increase over several weeks, after which a resident's chance of dominating a newcomer was about 90%.

The Nature of the Asymmetry in Contests with Prior Residents

The gradual development of an influence of prior residence indicates that it does not depend on an arbitrary, conventional asymmetry between opponents. A non-arbitrary asymmetry, either in relative payoffs or in fighting abilities as a result of residence, would require some time to develop. In great tits, *Parus major*, for instance, the advantage of territorial birds in contests with intruders takes several days to develop fully (Krebs 1982). In these experiments, intruders were previous residents temporarily removed from their territories, rather than newcomers, but the relative advantage of current residents might have a similar basis in both cases. The costs of territorial defence for residents might decrease gradually as they established routine relationships with their neighbours. The costs of defending a particular area would thus be lower for a resident than for an intruder that faced undiminished initial costs of defence.

If conflicts were settled by means of an arbitrary, conventional asymmetry, then brief occupation of an area could confer an advantage in contests, as for speckled wood butterflies, *Pararge aegeria*, competing for sun flecks (Davies 1978). Any such conventional asymmetry requires a criterion for a decision that 'no one is here before me'. The optimal criterion should depend on the time expected for a resident and newcomer to detect each other. An individual with a criterion shorter than the expected time to detect a prior resident would risk challenging undetected residents and would thus experience more escalated contests. This individual would lose the advantage of a conventional settlement, which comes from avoiding costly escalated contests. On the other hand, an individual with a criterion longer than the expected time to detect a prior resident would lose opportunities to opponents with shorter criteria.

The time required for wintering white-throated sparrows arriving in a new location to detect a prior resident might well be longer than the few minutes that should suffice for speckled wood butterflies in sun flecks, but it is not likely to be more than a few hours or days at most. Thus the gradual development of an influence of prior residence over many days in our experiments is unlikely to represent an evolutionarily stable strategy for conventional settlement of contests. Our results suggest instead that prior residence influenced dominance in our experiments primarily through the development of non-arbitrary asymmetries.

How Does Residence Produce a Non-arbitrary Asymmetry in Captivity?

It remains uncertain what it is about an individual's residence in an aviary that tends to increase its ability to dominate opponents there. The arrangements of feeding dishes, shelter and perches in our aviaries were standardized, but the positions of the aviaries with respect to external objects and vegetation were not. Thus familiarity with a particular aviary might have depended on familiarity with the environment around the aviary as well as with the locations of food, perches or shelter actually used. If so, perceptual familiarity with a location would directly contribute to a bird's ability to dominate opponents there.

In the field, familiarity with an area might directly influence the payoffs of defending an area by increasing the current availability of food or access to refuges (see references in the Introduction). In addition, an individual's fighting abilities might increase if its ability to find food improved its nutritional state. These possibilities for direct consequences of familiarity with an area, however, were largely excluded in our experiments by the standardized arrangements of the aviaries. Thus in our experiments the mechanisms for any non-arbitrary asymmetries appear largely unrelated to the evolutionary explanations for them. Perceptual familiarity with an aviary might increase commitment in contests (or decrease diffidence), because in natural situations perceptual familiarity with an area might indicate its probable usefulness.

Intrinsic Influences on Dominance in Captivity

In the initial groupings in aviaries, dominance was decided by interactions between strangers in unfamiliar locations. This situation thus isolated intrinsic influences on dominance from any influences of social contexts and location. The only consistent correlate of dominance in this situation was wing length in groups sorted by age. In contrast, there was no association of dominance with wing length when birds were grouped by wing length to separate the sexes. These findings suggest that it was sex rather than wing length that influenced dominance. However, we could not definitely separate effects of sex and wing length in

these experiments, because we lacked independent determinations of sex. Our results revealed no consistent effects of age, cranial pneumatization, morph, or crown stripes on dominance in initial groupings.

These findings agree in part with those from a field study of dominance in this species in the same area (Piper & Wiley 1989a, 1991a). In that study, of possible intrinsic factors, only age and sex correlated with dominance. Although sex was determined independently by laparotomy, it still proved difficult to separate effects of sex and wing length because of their strong correlation. The finding that an individual's age failed to correlate with its dominance in our study suggests that some contextual correlate of age, in addition to age itself, might affect dominance in the field.

Previous studies of the correlates of dominance in captive white-throated sparrows and related species have often relied on observations of a few groups, with erratic results. For instance, two groups of more than 50 white-throated sparrows gave strikingly different results in analyses of the influence of morph on dominance within sex and age classes (Watt et al. 1984). Schlinger (1987) found no influence of morph on dominance but did find effects of wing length. In other species as well, groups vary in correlates of dominance (Watt 1986). An assessment of all potential intrinsic influences on dominance in aviaries requires replicated studies with many groups.

Because dominance relationships between strangers in initial groupings in captivity develop in the absence of the natural contexts for these interactions, these studies reveal only intrinsic mechanisms of dominance and thus do not necessarily reveal the mechanisms by which interactions are settled in natural situations. Experiments on captive individuals can, however, clarify the causality of correlations observed in the field. The present study has confirmed a possible mechanism for the correlation between location and dominance in a free-living population of white-throated sparrows: an individual's residence in a location gradually increases its ability to win contests with newcomers there.

ACKNOWLEDGMENTS

REFERENCES

Ambrose, H. W. 1972. Effect of habitat familiarity and toe-clipping on rate of owl predation in *Microtis pennsylvanicus*. *J. Mammal.*, **53**, 909–912.

Arcese, P. & Smith, J. N. M. 1985. Phenotypic correlates and ecological consequences of dominance in song sparrows. *J. Anim. Ecol.*, **54**, 817–830.

Archawaranon, M., Dove, L. & Wiley, R. H. 1991. Social inertia and hormonal control of aggression and dominance in white-throated sparrows. *Behaviour*, **118**, 42–65.

Balph, M. H. 1979. Flock stability in relation to social dominance and agonistic behavior in wintering dark-eyed juncos. *Auk*, **96**, 714–722.

Brown, J. L. 1963. Aggression, dominance, and social organization in the steller jay. *Condor*, **65**, 460–484.

Cristol, D. A., Nolan, Jr, V. & Ketterson, E. D. 1990. Effect of prior residence on dominance status of dark-eyed juncos, *Junco hyemalis*. *Anim. Behav.*, **40**, 580–586.

Davies, N. B. 1978. Territorial defence in the speckled wood butterfly (*Pararge aegeria*): the resident always wins. *Anim. Behav.*, **26**, 138–147.

Davies, N. B. & Houston, A. I. 1981. Owners and satellites: the economics of territorial defence in the pied wagtail *Motacilla alba*. *J. Anim. Ecol.*, **50**, 157–180.

Franke Stevens, E. 1988. Contests between bands of feral horses for access to fresh water: the resident wins. *Anim. Behav.*, **36**, 1051–1053.

Hammerstein, P. 1981. The role of asymmetries in animal contests. *Anim. Behav.*, **29**, 193–205.

Hammerstein, P. & Parker, G. A. 1982. The asymmetric war of attrition. *J. theor. Biol.*, **96**, 647–682.

Holberton, R. L., Hanano, R. & Able, K. P. 1990. Age-related dominance in dark-eyed juncos: effects of plumage and prior residence. *Anim. Behav.*, **40**, 573–579.

Hyatt, G. W. & Salmon, M. 1978. Combat in fiddler crabs *Uca pugilator*: a quantitative analysis. *Behaviour*, **65**, 182–211.

Isbell, L. A., Cheney, D. L. & Seyfarth, R. M. 1990. Costs and benefits of home range shifts among vervet monkeys (*Cercopithecus aethiops*) in Amboseli National Park, Kenya. *Behav. Ecol. Sociobiol.*, **27**, 351–358.

Krebs, J. R. 1982. Territorial defence in the great tit, *Parus major*: do residents always win? *Behav. Ecol. Sciobiol.*, **11**, 185–194.

McVey, M. E. 1988. The opportunity for sexual selection in a territorial dragonfly, *Erythemis simplicicollis*. In: *Reproductive Success* (Ed. by T. H. Clutton-Brock), pp. 44–58. Chicago: University of Chicago Press.

Maynard Smith, J. 1974. The theory of games and the evolution of animal conflicts. *J. theor. Biol.*, **47**, 209–221.

Maynard Smith, J. & Parker, G. A. 1976. The logic of asymmetric contests. *Anim. Behav.*, **24**, 159–175.

Metzgar, L. A. 1967. An experimental comparison of screech owl predation on resident and transient white-footed mice. *J. Mammal.*, **48**, 387–390.

Phillips, R. R. 1971. The relationship between social behaviour and the use of space in the benthic fish *Chasmodes bosquianus* Lacépede (Teleosti: Bleniidae) II. The effect of prior residency on social and enclosure behaviour. *Z. Tierpsychol.*, **29**, 289–408.

Piper, W. H. 1990a. Exposure to predators and access to food in wintering white-throated sparrows *Zonotrichia albicollis. Behaviour*, **112**, 284–294.

Piper, W. H. 1990b. Site-tenacity and dominance in wintering white-throated sparrows *Zonotrichia albicollis* (Passeriformes: Emberizinae). *Ethology*, **85**, 114–122.

Piper, W. H. & Wiley, R. H. 1989a. Correlates of dominance in wintering white-throated sparrows: age, sex and location. *Anim. Behav.*, **37**, 298–310.

Piper, W. H. & Wiley, R. H. 1989b. Distinguishing morphs of the white-throated sparrow in basic plumage. *J. Field Ornithol.*, **60**, 73–83.

Piper, W. H. & Wiley, R. H. 1990a. The relationship between social dominance, subcutaneous fat and annual survival in wintering white-throated sparrows (*Zonotrichia albicollis*). *Behav. Ecol. Sociobiol.*, **26**, 201–208.

Piper, W. H. & Wiley, R. H. 1990b. Correlates of range size in wintering white-throated sparrows, *Zonotrichia albicollis. Anim. Behav.*, **40**, 545–552.

Piper, W. H. & Wiley, R. H. 1991a. Errata: correlates of dominance in white-throated sparrows. *Anim. Behav.*, **42**, 339.

Piper, W. H. & Wiley, R. H. 1991b. Effects of laparotomies on wintering white-throated sparrows and the usefulness of wing chord as a criterion for sexing. *J. Field Ornithol.*, **62**, 40–45.

Riechert, S. E. 1978. Games spiders play: behavioural variability in territorial disputes. *Behav. Ecol. Sociobiol.*, **3**, 135–162.

Schlinger, B. A. 1987. Plasma androgens and aggressiveness in captive winter white-throated sparrows (*Zonotrichia albicollis*). *Horm. Behav.*, **21**, 203–210.

Schneider, K. C. J. 1984. Dominance, predation and optimal foraging in white-throated sparrow flocks. *Ecology*, **65**, 1820–1827.

Schwabl, H. Ramenovsky, M., Schwabl-Benzinger, I., Farner, D. S. & Wingfield, J. C. 1988. Social status, circulating levels of hormones, and competition for food in winter flocks of the white-throated sparrow. *Behaviour*, **107**, 107–121.

Watt, D. J. 1986. Relationship of plumage variability, size and sex to social dominance in Harris' sparrows. *Anim. Behav.*, **34**, 16–27.

Watt, D. J., Ralph, C. J. & Atkinson, C. T. 1984. The role of plumage polymorphism in dominance relationships of the white-throated sparrow. *Auk*, **101**, 110–120.

Wiley, R. H. 1990. Prior residence and coat-tail effects in dominance relationships of male dark-eyed juncos, *Junco hyemalis. Anim. Behav.*, **40**, 587–596.

Wiley, R. H. 1991. Both high- and low-ranking white-throated sparrows find novel locations of food. *Auk*, **108**, 8–15.

Wiley, R. H. & Piper, W. H. 1992. Timing of cranial pneumatization in white-throated sparrows. *Condor*, **94**, 336–343.

Wiley, R. H. & Wiley, M. S. 1980. Territorial behavior of a blackbird: mechanisms of site-dependent dominance. *Behaviour*, **73**, 130–154.

Wilkinson, L. 1988. *Systat: the System for Statistics.* Evanston, Illinois: SYSTAT.

Yasukawa, K. & Bick, E. I. 1983. Dominance hierarchies in dark-eyed juncos (*Junco hyemalis*): a test of a game theory model. *Anim. Behav.*, **31**, 439–448.

Zach, R. & Falls, J. B. 1976. Influence of capturing a prey on subsequent search in the ovenbird (Aves: Parulidae). *Can. J. Zool.*, **55**, 1958–1969.

Zayan, R. C. 1975. Modification des éffets liés a priorité de residence chez *Xiphophorus* (Pisces: Poeciliidae): le role des manipulations experimentales. *Z. Tierpsychol.*, **39**, 463–491.