



Should I Stay or Should I Go Now: Late Establishment and Low Site Fidelity as Alternative Territorial Behaviors

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Abstract

In species in which males defend territories for breeding, males may differ in territorial behavior; alternative behaviors among territorial males are not well understood. In our long-term study of partially-migratory song sparrows, we have observed that most territorial males establish territories before females begin nesting and remain site-faithful both within and between breeding seasons; however, some males establish territories later in the season (late establishers) and/or change territory locations either within or between seasons (movers). Whether late establishment or moving are equally successful strategies for territory defense, or best-of-bad-job options, is not known. Here, we compare the frequencies of these behaviors to demographic variables over a 9-yr period and compare lifetime tenure and early season nesting success for males who differ in site fidelity and timing of territory establishment. Across years, late establishing was negatively correlated with the return rate of previously territorial males; moving was positively correlated with the number of occupied territories at the start of the breeding season (territory density). While moving was independent of number of years on territory, late territory establishment only occurred in a male's first year as a territory holder. Of 88 males, 25% established their first territory late, primarily in undefended space; 31% moved. Late and early establishers did not differ in lifetime tenure; movers, however, had longer lifetime tenure than site-faithful males. Among early establishers, movers and non-movers did not differ in the number of successful early nests/year or number of young fledged/year; among late establishers, however, movers had significantly higher early nesting success by both measures. Late establishers who moved had higher early season nesting success and higher early season nesting success/year than site-faithful early establishers. Thus, individual variation in the timing of territory establishment and site fidelity may be facultative alternative territorial strategies.

Introduction

In species in which males defend territories for breeding, successfully establishing and maintaining a territory can be critical for reproductive success (Carpenter 1958; Brown & Orians 1970). High-quality

habitat may not be available for all males, however; thus, a common feature of territorial systems is the presence of floaters – non-territorial individuals who either wait for territorial openings or attempt to overthrow territorial individuals (Brown 1969; Smith 1978; Arcese 1989; Smith & Arcese 1989; Stutchbury

1991; Sergio et al. 2009; Penteriani et al. 2011). Being a floater is typically seen as a best-of-a-bad-job strategy, as floaters typically suffer lower reproductive success than territorial individuals (reviewed in Sardell et al. 2010; but see Ewen et al. 1999; Kempenaers et al. 2001); however, some territorial systems may include non-territorial individuals with reproductive success equal to territorial individuals (Raihani et al. 2008). While non-territorial alternatives to territorial behavior have been well documented, alternative behaviors among territorial males, such as differential investment in territory defense (Tuttle 2003), are less well known. Here, we determine the consequences of individual variation in the behavior of territorial males, specifically timing of territory establishment and site fidelity, in a partially-migratory population of song sparrows (*Melospiza melodia*).

Timing of territory establishment is predicted to be critically important in territorial systems: earlier establishing individuals are likely to have access to higher quality territories (Kokko 1999), and earlier arriving individuals also have the opportunity to develop familiarity with the site sooner, which may be beneficial if either familiarity or prior residency confer a competitive advantage (Maynard Smith 1974; Stamps & Krishnan 1999, 2001). Thus, it is not surprising that earlier territory establishment can significantly increase seasonal reproductive success (Brooke 1979; Low et al. 2007). On the other hand, late territory establishment may provide a delayed benefit if newcomers are subsequently more successful having gained familiarity with the site (Yasukawa 1979). In addition, if otherwise high-quality individuals arrive on the breeding grounds too late to obtain a high-quality territory, alternative strategies may be favored (Zack & Stutchbury 1992; Lee 2005).

High site fidelity is typical of many territorial species, especially for males defending breeding territories (Greenwood & Harvey 1982). While females may switch territories to increase access to resources or in response to failed breeding attempts (Wauters et al. 1995), males are often less likely than females to relocate following reproductive failure (Howlett & Stutchbury 2003; Sedgwick 2004; Middleton et al. 2006; Linkhart & Reynolds 2007). Site fidelity, especially between-year fidelity to a specific territory location (i.e. territory fidelity, sensu Hoover (2003)), is thought to be advantageous because site-faithful individuals benefit from familiarity with habitat (reviewed in Greenwood & Harvey 1982) and from established relationships with neighbors (Getty 1987;

Temeles 1994), enabling differential responses to threats from different neighbors (Switzer & Eason 2003; Hyman & Hughes 2006; Akçay et al. 2009). In some songbird populations, males learn the songs of their future territorial neighbors (Beecher et al. 1994), allowing for shared songs to be used as graded signaling during aggressive interactions (Krebs et al. 1981; Burt et al. 2001; Beecher & Campbell 2005). Territorial relocation, even if it increases territorial quality, may thus be costly for males, as moving would result in a loss of this established social network. Nonetheless, males in some territorial species do relocate their territories in response to variation in breeding success or to obtain a territory of higher quality (Brooke 1979; Haas 1998; Hoover 2003). In other cases, however, territory relocation may be a reflection of low resource holding potential: males unable to defend their territories may be forced off, particularly if their territory is high quality and thus subject to frequent territorial intrusions (Arcese & Smith 1988).

Song sparrows are a widespread territorial songbird with considerable geographic variation in territorial behavior, ranging from year-round territoriality in resident populations (Tompa 1962; Arcese 1989) to seasonal territoriality in migratory or partially migratory populations (Nice 1934); territorial males may be highly site-faithful in some populations (Tompa 1962; Beecher 1996), while others show very low site fidelity (Weatherhead & Boak 1986). In our long-term study of partially migratory song sparrows in northwestern Pennsylvania (Hughes et al. 2007), we have observed individual variation in both site fidelity and timing of territory establishment. Such variation may reflect options of last resort: males that establish territories late in the breeding season may be unable to compete successfully with other males to obtain a territory before the breeding season; males who are not site-faithful may move because they are unable to defend the same territory they held previously. Alternatively, late establishment and territory relocation may be facultative alternative strategies for territorial defense. In this study, we test whether these territorial behaviors are more likely to occur in males who are less able to compete for high-quality territories. In addition, we compare the frequency of territory relocation and late establishment to population demographic variables over a 9-yr period. If late establishment and/or territory relocation are behaviors of last resort for males with low territory-holding ability, we predict that these males will hold territories for shorter times at the site (lower lifetime

tenure) and will have lower nesting success; these males may also be smaller and in lower condition than other males. Furthermore, we predict that these behaviors will occur more frequently in years with a higher percentage of returning males and higher territorial densities (years with greater competition for space).

Methods

The focal site is approx. 11 ha area within a managed state game land in Crawford County, PA (41°33'N, 80°22'W, see Hughes et al. 2007 for description). The site is bounded on the north and south by shallow wetlands and is connected to land by narrow isthmuses on the east and west; thus, it is not an isolated population but is contiguous with additional song sparrow habitat, facilitating dispersal into and out of the site, but with the exception of the outermost territory holders on each isthmus, territorial interactions are limited to other males at the site. Song sparrows in this population are partially migratory, with some individuals remaining on or near their territories throughout the winter and some migrating at least as far south as North Carolina (Hughes et al. 2007). Some males are defending territories by early Mar., while others arrive in early to mid-April. Females begin building nests in mid-late April, and the median date of first nest hatch is May 13 (Hughes, pers. obs.). At least some pairs continue to re-nest through at least mid-July (Hughes, pers. obs.) and possibly into Aug. (Nice 1932; Todd 1940). However, vegetation at the site becomes extremely dense by mid-summer, resulting in measures of nesting success that are likely to be biased to territories with more open habitat (i.e. shorter grass, fewer dense shrubs). Here, we use early season nesting success as an estimate of overall nesting success; for the years included in this study (1998–2008), the average date of last field observation is June 24. Although not a complete record of nesting success, early season nesting success is likely to be a useful estimate of overall nesting success for two reasons. First, pairs that are successful early in the season have ample time to re-nest and have been observed to do so (Hughes pers. obs.). Second, young fledging earlier in the breeding season may be more likely to survive to recruit and/or be dominant to later hatched young (Arcese & Smith 1985; Nilsson & Smith 1988; Low et al. 2007), suggesting that early season nests may have a greater impact on overall reproductive success than late season nests. Nonetheless, late season reproductive effort is

unlikely to be independent of early season success or clutch size (Hauber 2002, 2006); thus, pairs that are successful early in the season may be less able to invest in later season broods, while pairs who have not been successful early in the season may be able to offset early failures with later success. Thus, limitations of using early season nesting success as metric of success need to be considered when interpreting the results.

Song sparrows are typically socially monogamous, with males performing the majority of territorial defense (Nice 1937). All territorial males within this site have been banded with a US Fish and Wildlife Service aluminum band and a unique combination of three color bands since 1999; in 1998, approximately half of the field site was banded. The oldest known male at the site was at least 9 yr old during his last year of tenure but was banded before territory monitoring began and so may not have been territorial throughout that time; the longest known tenures at the site are 7 yr ($n = 4$). The sample used for this study includes all males known to have initiated their territory tenure at the site from 1998 to 2005; this sample includes 88 males, 84 with full known tenure, and 4 who were still on-site at the end of the 2008 breeding season (tenure of birds still on-site = 4–7 yr). Unless previously captured and banded as a floater ($n = 5$ in this data set), males are captured and banded in their first year of tenure; tarsus length (right tarsus, measured with digital calipers ± 0.01 mm) and mass (± 1.0 g, measured with 60 g spring scale) are measured at this time. Three males in this data set were originally banded as nestlings; these individuals were recaptured in their first year of tenure for the measures above. Tarsus length and mass were used to determine whether males differing in time of establishment and/or site fidelity differed in size (tarsus length) or condition (residuals from regression of mass \times tarsus). It is important to note that these morphological measures are a snapshot of male size and condition in his first year of territory tenure, but as birds were not re-captured annually, these variables do not measure potential variation in condition.

Each male was categorized in terms of timing of territory establishment and site fidelity, as follows: a male was considered to have established a territory if he was observed singing uncontested by other males in the same location for at least 5 d; late territory establishment was defined as establishing a territory after the first nest at the site that year has hatched but before the end of June. Late territory establishment, then, does not preclude successful

nesting in that year, if the male is able to obtain a female. As late territory establishment was only observed for males in their first year on territory, we categorized males as 'late establishers' if they established their first territory at the site after hatching begins.

With regard to site fidelity, most territorial males in the population are site-faithful, defending a territory that is identical to, or substantially overlaps with, the territory held the previous year. For the purpose of this study, males were categorized as 'movers' if they defended more than one non-overlapping territory over the course of their tenure. Categorizing a male as a mover based on a single territory relocation may obscure variation among movers in their degree of site fidelity; however, given that most territory relocations happen between seasons and the median territory tenure is two seasons, even one move represents low site fidelity. To determine whether the classification of males as early or late establishers was independent of their classification as movers or non-movers, we used a chi-squared test.

With each male classified as to time of first territory establishment and site fidelity, we performed two-way ANOVAs of establishment time and site fidelity separately on three measures of lifetime territorial success: lifetime territorial tenure (calculated as total number of years on territory at the site, regardless of number of territories held), lifetime successful nests (defined as the number of nests from which at least one young fledges), and lifetime young fledged. Number of young fledged is based on the number of young in successful nests at day 6–7 because disturbing the nest at 8 d of age can result in premature fledging. Comparing nestling counts from hatch to day 6–7, partial predation is rare in this population. In a few cases ($n = 8$), parents were observed feeding fledglings before the nest could be found; in these cases, the median number of young from successful nests (4) was used in the analysis. As noted earlier, these latter measures are limited to nesting success in the first half of the season. Finally, as males with longer tenures have more opportunities for early season nesting success, we also analyzed the number of successful early season nests and number of early season young fledged per year. As we were unable to transform nests/year and young/year to meet the assumptions of an ANOVA, and as the previous analyses suggested that the effects of moving are different for early and late establishers, we performed Mann–Whitney *U*-tests on these latter two variables comparing movers and

non-movers separately for early and late establishers. As our measures of territorial success (lifetime tenure, number of successful nests, number of young fledged, number of successful nests/year and number of young fledged/year) are obviously not independent, we evaluated statistical significance in these seven tests using the sequential Bonferroni method (Rice 1989).

Because most territorial relocations occurred between breeding seasons, males with lifetime tenure ≤ 1 yr are over-represented among the non-movers and may unduly influence comparisons between movers and non-movers. For this reason, we also repeated the above analyses including only males with lifetime tenure > 1 . With tenure ≤ 1 males removed, the variables nests/year and young/year better conformed to the assumptions of an ANOVA, so we used the same statistical approach (two-way ANOVA) as with the other variables. As above, we evaluated significance using the sequential Bonferroni method (Rice 1989).

To determine whether the frequency of either late territory establishment or territory relocation was correlated with population demographics, we determined whether the number of males who moved or who established their territory after the onset of breeding was correlated with either return rate or territory density at the beginning of the breeding season. Return rate for territorial males is defined as the percentage of territorial males who return to be territorial the subsequent year; this measure includes all males observed to be territorial in the previous year, even if they apparently lost their territory during the breeding season, as males have been observed to return to their territories the year following such 'losses'. Territory density at the beginning of the breeding season is defined as the number of territories at the site at the beginning of the breeding season. Because 1999 was the first year in which the entire site was banded, 2000 was the first year for which return rate could be calculated; thus, the analysis of population demographics included 9 yr: 2000–2008.

Where possible, data were transformed as necessary to meet the assumptions of normality and homoscedasticity. As noted above, for the analyses of nests/year and young/year using the complete data set, we were unable to successfully transform the data to meet these assumptions; therefore, non-parametric tests were used. All statistical analyses were performed in Systat. Permits for banding were issued by the US Geological Survey and Pennsylvania Game Commission; the Pennsylvania Game

Commission also provided a Special Use Permit for Scientific Study, for access to the game lands. This work was covered under IACUC protocols from Princeton University (protocols 1312, 1312-AR2) and the College of Charleston (protocols 02-014, 05-002, 08-002).

Results

All instances of late territory initiation occurred in the first year of a male's tenure; all returning males initiated territorial behavior well before the first nest in the population hatched. Of the 88 males in this sample, 22 (25%) were late establishers in their first year. These late-establishing males primarily set up territories in undefended space (either previously vacant or following the disappearance of a territorial male, $n = 15$, 68%), or invaded (either directly or by inserting adjacent to and encroaching on) the territory of a male feeding young ($n = 5$, 23%). Only two males established territories late in the breeding season by invading or encroaching on the territory of a male not feeding young. When the sample was expanded to include all late-establishing males in the 1998–2008 breeding seasons (late establishers in 2006–2008 not included in other analyses because their full tenure is not known), the same pattern was found: of a total of 35 late-establishing males, 20 (57%) established territories in undefended space, 13 (37%) invaded the territories of males feeding young, and 2 (6%) invaded the territories of males not feeding young.

Of the 88 males in the sample, 27 (31%) defended more than one non-overlapping territory over the course of their tenure. A few males ($n = 5$, or 19% of movers) moved more than once; overall, of 120 'bird-returns,' 30 (25%) were to a territory non-overlapping with the previous year. Most instances of territory relocation occurred when males returned to a new territory at the start of the next breeding season (rather than during breeding seasons); only 3 of 27 movers (11% of movers; 3.4% of entire sample) moved during the breeding season. Given that most moves occur between seasons, males whose lifetime tenure is 1 yr or less were primarily non-movers: of the 35 males with a lifetime tenure ≤ 1 , only 2 (6%) were movers; of the 53 males with a lifetime tenure > 1 , 25 (47%) were movers.

Most territory movements were of relatively short distance. Two males relocated gradually, shifting their territories each season such that no single return was to a non-overlapping territory, but over the course of their tenure, they defended at least

two territories that did not overlap; the largest distance between non-overlapping territories for these two birds was 1 and 2 territories, respectively. The remaining 23 between-year movers moved on average 1.9 territories (range = 1–4). Nonetheless, it is possible that longer moves are missed because the male moved out of the study site, leading to underestimates not only of distance, but of the percentage of males who move; one male in this sample was 'rediscovered' at another location, after already moving once within the study site.

Moving can occur at any time in a male's tenure: the observed number of birds moving in any year of tenure was independent of year of tenure ($\chi^2_2 = 0.168$, $p = 0.919$; years 4 and higher combined for analysis). Among movers, there was no difference in number of successful early season nests/year on the old and new territory (between-year movers $N = 23$, successful nests/year on old territory = 0.27 ± 0.083 ($\bar{x} \pm SE$), successful nests/year on new territory = 0.19 ± 0.07 , paired $t_{22} = 0.644$, $p = 0.526$). Six movers moved to a new territory following a season in which they successfully fledged young early in the season; all but one of these 'move following success' birds were in their first year on territory, and none of them had another successful nest during the study period (May–June) on their new territory ($N = 6$, successful nests/year on old territory = 0.83 ± 0.105 ; successful nests/year on new territory = 0 ± 0). In contrast, for birds whose territorial relocation followed an unsuccessful season, the average number of successful early season nests/year was nearly four times greater on the new territory ($N = 17$, successful nests/year on old territory = 0.07 ± 0.045 , successful nests/year on new territory = 0.26 ± 0.088 , paired $t_{16} = -2.107$, $p = 0.051$).

Moving was statistically independent of timing of first territory establishment ($\chi^2_1 = 1.443$, $p = 0.230$): of the 66 early establishing males, 18 (27%) subsequently moved to a non-overlapping territory at least once during their tenure; of the 22 late-establishing males, 9 (41%) subsequently moved their territory. The same result was obtained when the analysis was restricted to males with tenure > 1 : territory relocation was not significantly associated with timing of first territory establishment ($\chi^2_1 = 0.759$, $p = 0.384$); of the 39 early establishing males with tenure > 1 , 17 subsequently moved (44%); of the 14 late-establishing males with tenure > 1 , eight subsequently moved (57%).

For all males in this data set combined ($N = 88$), tenure ranged from 0.5 to 7 yr [2.26 ± 1.6 ,

($\bar{x} \pm SD$)]. Males who moved had longer territory tenure than site-faithful males (analysis performed on square root-transformed data to meet the assumptions of the ANOVA; $F_{1,84} = 29.739$, adjusted $p < 0.001$, Fig. 1); neither time of establishment ($F_{1,84} = 0.295$, $p = 0.589$) nor the interaction between site fidelity and time of establishment ($F_{1,84} = 1.635$, $p = 0.205$) were significant. Because most changes in territorial location occur between years, the greater tenure times for movers may simply reflect the fact that most males with tenure of only 1 yr are non-movers. However, when the analysis was restricted to only males with tenure >1 yr (to males, in other words, who all have the opportunity to change territory locations between seasons), the result was the same. Among males with tenure >1 yr, males who moved had longer territory tenure than site-faithful males (analysis performed on square root-transformed data; $F_{1,49} = 7.024$, adjusted $p = 0.033$); neither time of establishment ($F_{1,49} = 0.099$, $p = 0.754$) nor the interaction between site fidelity and time of establishment ($F_{1,49} = 2.197$, $p = 0.145$) were significant.

For all males in this data set combined ($N = 88$), the lifetime number of successful nests early in the season ranged from 0 to 3 [0.49 ± 0.709 ($\bar{x} \pm SD$)]; the lifetime number of young fledged early in the season ranged from 0 to 13 [1.99 ± 2.883 ($\bar{x} \pm SD$)]. For both number of successful early season nests and number of early season young fledged, there were significant interactions between time of first territory establishment and site fidelity (both analyses performed on log-transformed data; nests: $F_{1,84} = 10.764$, adjusted $p = 0.009$, Fig. 2a; young: $F_{1,84} = 8.906$, adjusted $p = 0.019$, Fig. 2b). By both

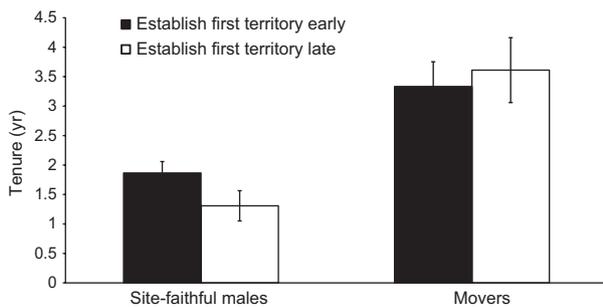


Fig. 1: Territory tenure and variation in territorial behavior; $\bar{x} \pm SE$. Males that defend more than one non-overlapping territory during their tenure have longer tenure times than males that are site-faithful. (Sample sizes: early establishing, site-faithful = 48; early establishing movers = 18; late establishing, site-faithful = 13; late-establishing movers = 9.)

measures, among early establishing males, there was no difference in lifetime early season nesting success of movers and non-movers; however, late-establishing males who subsequently moved had higher success than late establishers who were site-faithful. By both measures, the males with highest success were late-establishing males who subsequently moved; the average number of early season young fledged by late-establishing movers was over three times greater than early establishing non-movers (late-establishing movers ($\bar{x} \pm SE$) = 5.8 ± 1.49 ; early establishing non-movers = 1.7 ± 0.37 , Fig. 2b). As with the analysis of tenure, when the analysis of nesting success was restricted to males with tenure >1, the same result was obtained [both analyses performed on log-transformed data; significant interactions between time of first territory establishment and site fidelity for nests ($F_{1,49} = 9.314$, adjusted $p = 0.018$) and young ($F_{1,49} = 7.967$, adjusted $p = 0.027$)].

However, as we only consider early season nests here, much of the variation between birds in nesting

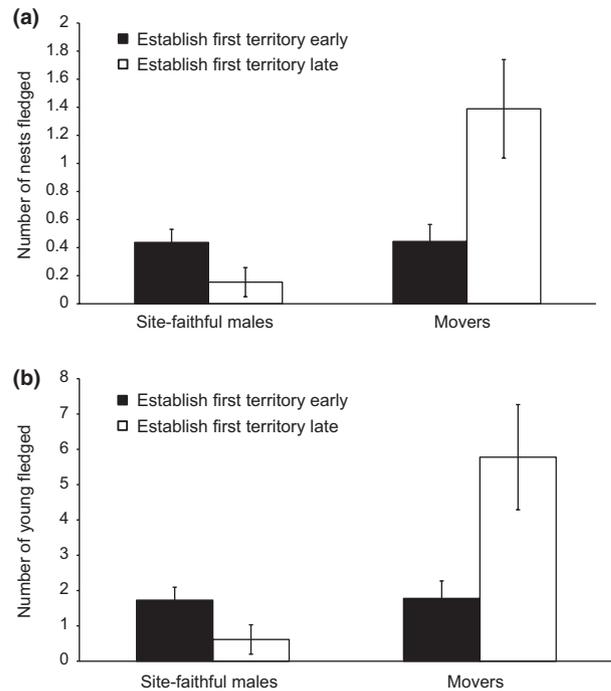


Fig. 2: Lifetime early season nesting success [number of successful nests (a) and number of young fledged (b)] and variation in territorial behavior; $\bar{x} \pm SE$. There is a significant interaction between first territory establishment time and site fidelity: for males establishing their first territory early in the season, there is no difference in nesting success between movers and site-faithful males; however, for late establishers, movers have higher nesting success than non-movers. (Sample sizes as in Fig. 1.)

success is likely to be because of differences in tenure; to determine whether these males differed in early season nesting success/years on territory, we compared successful early season nests/year and early season young fledged/year between movers and non-movers. As the above analysis suggests that moving had different effects on nesting success in early and late establishers, we performed this analysis separately for early and late establishers. For all males in the data set combined, the number of successful early season nests/year ranged from 0 to 2 [0.21 ± 0.34 ($\bar{x} \pm SD$)]; the number of early season young fledged/year ranged from 0 to 10 [0.86 ± 1.52 ($\bar{x} \pm SD$)]. For early establishing males, neither the number of early season successful nests/year ($U = 444$, $N_1 = 48$, $N_2 = 18$, $p = 0.844$, Fig. 3a) nor number of early season young fledged/year ($U = 437$, $N_1 = 48$, $N_2 = 18$, $p = 0.935$, Fig. 3b) differed between movers and non-movers. For late-establishing males, however, movers had more successful early season nests/year ($U = 23$, $N_1 = 13$,

$N_2 = 9$, adjusted $p = 0.023$, Fig. 3a) and fledged more early season young ($U = 22.5$, $N_1 = 13$, $N_2 = 9$, adjusted $p = 0.028$, Fig. 3b) than non-movers. Only one mover (a late-establishing male) failed to obtain a female on the new territory; thus, the different effects of moving for late and early establishing males is unlikely to be because of differences in ability to attract a female. When this analysis was restricted to males with tenure >1 , the 2-way ANOVA confirmed the same pattern, with significant interactions between time of first territory establishment and site fidelity for both nests/year ($F_{1,49} = 5.09$, adjusted $p = 0.041$) and young/year ($F_{1,49} = 5.707$, adjusted $p = 0.021$).

At time of capture, males establishing territories early were neither larger nor in better condition than males establishing territories late; similarly, site-faithful males were neither larger nor in better condition than males who relocated. Neither early and late males ($F_{1,82} = 0.001$, $p = 0.973$) nor movers and non-movers ($F_{1,82} = 2.485$, $p = 0.119$) differed in tarsus length; the interaction between time of establishment and site fidelity was also not significant ($F_{1,82} = 0.627$, $p = 0.431$). The residuals of mass \times tarsus also did not differ between any group (time of establishment: $F_{1,81} = 0.090$, $p = 0.764$; site fidelity: $F_{1,81} = 1.082$, $p = 0.301$; interaction: $F_{1,81} = 2.026$, $p = 0.158$).

Across the 9 yr of this study, both the number of late-establishing males and the number of males moving to new territory locations within each year were correlated with population demographics. The number of late-establishing males in a given year was negatively correlated with return rate from the previous year ($r = -0.815$, $N = 9$, $p = 0.007$, Fig. 4a), but was not related to population density (number of territories present at the beginning of the season: $r = -0.294$, $N = 9$, $p = 0.443$, Fig. 4b). Conversely, the number of movers was positively correlated with population density ($r = 0.813$, $N = 9$, $p = 0.008$, Fig. 4c), but not with return rate from the previous year ($r = 0.564$, $N = 9$, $p = 0.114$, Fig. 4d). Late territory establishment and territory relocation were not correlated ($r = -0.565$, $N = 9$, $p = 0.113$) – that is, years with high levels of one of these behaviors did not consistently have high or low levels of the other – and population density was not correlated with return rate from the previous year ($r = 0.321$, $N = 9$, $p = 0.400$). Thus, territory relocation was most common when territory density was high at the beginning of the breeding season, but late territorial establishment was most

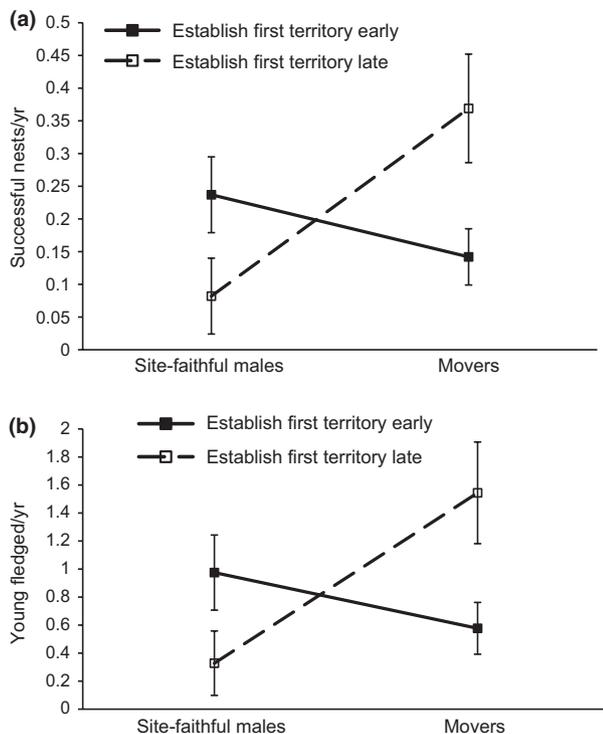


Fig. 3: Nesting success/year [number of successful nests/year (a) and number of young fledged/year (b)] and variation in territorial behavior; $\bar{x} \pm SE$. For early establishing males, there is no difference between movers and site-faithful males in nesting success/year; for late establishers, however, movers have more successful nests/year and fledge more young/year than non-movers. (Sample sizes as in Fig. 1.)

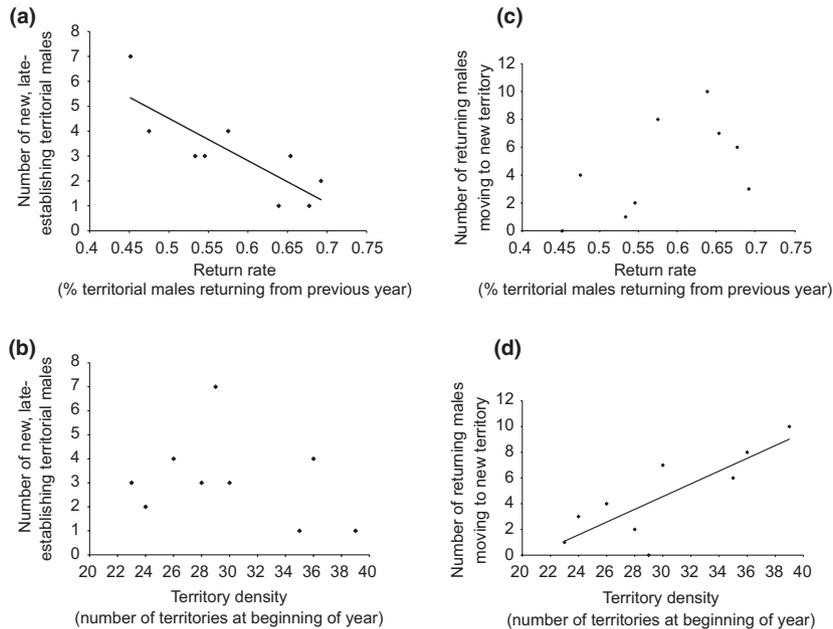


Fig. 4: Population demographics and variation in territorial behavior ($N = 9$ yr; 2000–2008). (a) The number of first-year males who establish territories late in the season is negatively correlated with the return rate of previously territorial males. (b) The number of first-year males who establish territories late in the season is independent of territory density. (c) The number of males moving to new territories is independent of return rate. (d) The number of males moving to new territories is positively correlated with territory density.

common when the return rate of previously territorial males was low.

Discussion

Alternative territorial behaviors are known in many systems, ranging from cases in which each behavioral phenotype results in equal reproductive success (Tuttle 2003; Raihani et al. 2008), to non-territorial best-of-a-bad-job strategies (e.g. floaters, Smith 1978; Smith & Arcese 1989). At our study site, as is typical in many territorial systems, most territorial song sparrows establish territories well before the breeding season begins and remain site-faithful throughout their tenure. Nonetheless, 25% of territorial males in this study initiated territory defense in their first year by invading or inserting after nests have begun to hatch; similarly, 31% of males moved, defending more than one non-overlapping territory during their tenure. However, males engaging in these territorial behaviors did not differ in size or condition from other males in the population, at least at the outset of their territorial tenure; moreover, they had territory tenures as long or longer, and lifetime early season nesting success as high or higher than other males at the site. In fact, late-establishing males who later moved to a new territory had the highest lifetime early season nesting success at the site. Rather than being the last resort for males unable to establish and maintain territo-

ries, late establishment and low site fidelity appear to be successful alternative territorial behaviors.

While neither time of first territory establishment nor site fidelity were related to male condition (at least at the outset of his tenure), both moving and late establishment were correlated with population demographics (Fig. 4). Together, these results suggest facultative behaviors influenced by environmental conditions, rather than intrinsic alternative male strategies. Late establishment was not correlated with territory density, but was negatively correlated with the return rate of territorial males from the previous year. In other words, late establishment occurred more commonly not when competition was high, but when the competitors included fewer experienced territorial males; such a pattern suggests opportunistic behavior. In contrast, the number of males moving was positively correlated with territory density; moving occurred more frequently when there was more competition for space. Territory density is also correlated with the number of new males in the population (Hughes, unpub. data); years with higher territory density, then, are also years with a greater number of inexperienced males, and returning males may have a competitive advantage. Thus, moving appears to occur more frequently when there is higher competition, and increased opportunities for experienced males to compete for territories.

Late and early establishers did not differ in site fidelity; however, the consequences of low site fidel-

ity differed between early and late-establishing males. While both early and late-establishing movers had longer tenure than site-faithful males (Fig. 1), only late-establishing movers (not early establishing movers) had higher lifetime early season nesting success (Fig. 2) and nesting success/year (Fig. 3) than site-faithful males. This interaction between time of first territory establishment and site fidelity is unexpected and will require further data to fully understand. Males engaging in these different territorial behaviors may differ in migratory status and/or whether they are immigrants to the site; a better understanding of both natal and adult dispersal into the site may be useful in understanding variation in territorial behavior and its consequences. Another possible explanation for this difference between early and late-establishing movers could be male condition: although we did not find differences in condition in the first year of tenure, we did not re-measure males in later years, so we cannot rule out condition differences among older males. If early and late-establishing movers tend to differ in condition in their subsequent years of tenure, such a difference may account for the observed differences between these males in lifetime early season nesting success. Finally, differences between early and late-establishing movers in lifetime early season nesting success may also be related to the quality of territory obtained; clutch size in song sparrows is influenced by the resources available on or near the territory (Arcese & Smith 1988), and nest failure is due almost entirely to predators, which may not be uniformly distributed across territories. However, early season nesting success may not reflect the overall quality of the territory, as changes in resources across the season may allow some territories to produce more young later in the season. Thus, it is not yet clear whether the higher early season nesting success of late-establishing movers is because of differences in condition between early and late-establishing males in later years of their tenure, differences in the quality of territories obtained by early and late-establishing males when they move, or to other factors not yet explored.

Similarly, it is not known whether the success of late-establishing movers early in the season leads to higher reproductive success for these males. Other males, such as early establishing site-faithful males, may have higher late season success or greater success obtaining extra-pair young, thus offsetting the higher early season success of late-establishing movers. Studies in other song sparrow populations (Arcese & Smith 1985) and other species (Nilsson &

Smith 1988; Low et al. 2007) have found that early season young may be more valuable, in that they are more likely to be dominant and/or survive to recruit; however, whether early season young are similarly more likely to contribute to lifetime reproductive success in this population is not known. Most extra-pair paternity in song sparrows is attributable to territorial neighbors (O'Connor et al. 2006; Sardell et al. 2010; Hill et al. 2011); late-establishing males, because they are not yet territorial during the first round of female fertility during their first year, may thus be less able to acquire extra-pair fertilizations in their first year. As with late season young, late-establishing movers may obtain fewer extra-pair young than males engaging in other territorial behaviors, thus offsetting their higher lifetime early season nesting success; whether such differences between territorial behaviors in late season and/or extra-pair young results in differences in lifetime reproductive success remain to be explored.

Regardless of whether variation in these territorial behaviors (timing of first territory establishment, site fidelity) is associated with variation in lifetime late season and/or extra-pair success, it is clear that variation in these territorial behaviors is associated with variation in tenure and early season nesting success. Furthermore, males who both establish late and subsequently move had the highest early season success at the site. Late territory establishment and territory relocation, then, are likely facultative variants in territorial behavior that cannot be dismissed as aberrant or indicative of low-quality males.

Timing of Territory Establishment

Late establishers may benefit by reducing the costs of territorial behavior in their first year. First, whereas most males initiate territorial behavior as early as Mar., males that initiate territorial behavior in late May or June are expending energy on territory defense for 2–3 mo less in their first year (assuming that they are not more likely to extend their territory defense longer at the end of the season). Second, nearly all late establishers set up their territories either in previously undefended space or invade territories with males engaged in parental care, in either case potentially reducing the effort necessary for territory establishment. Finally, only first-year males were observed to establish territories late in the season; if there is a competitive advantage of prior residency (Maynard Smith 1974) or if experienced birds return earlier from migration, first-year males are expected to be at a competitive disadvan-

tage and are likely to have fewer, lower quality options for territories. As predicted by Lee's (2005) model of alternative territorial behavior, such males may choose to forgo territorial behavior early in the season, gambling on their ability to acquire a higher quality territory later in the season. Nearly 40% of late establishers invaded the territories of males feeding young. Males that delay territorial behavior and are subsequently successful in evicting an owner engaged in parental care may be able to obtain a high-quality territory in their first year for relatively low costs.

Nonetheless, clearly not all late establishers acquire high-quality territories; given that more than half of late establishers set up territories in previously undefended space, a cost of late establishment for these males may be the risk of obtaining a territory of reduced territory quality. Although late establishment and territory relocation were not significantly associated, 41% of late establishers eventually moved to a new territory, as compared to 27% of early establishing males. In wheatears (*Oenanthe oenanthe*), younger males are relegated to lower quality territories; as males age, they move to higher quality territories with higher reproductive output (Brooke 1979). Territory relocation by late-establishing males in our song sparrow population may similarly reflect attempts to move from previously unoccupied (and presumably low quality) to higher quality territories. The early season nesting success data are consistent with this interpretation: when site-faithful, late establishers had lower early season nesting success than early arriving males; when they moved, however, late establishers had higher early season nesting success than any other territorial strategy (Fig. 2), and significantly increased the number of successful early season nests/year and early season young fledged/year (Fig. 3).

Another possible cost of late establishment is an opportunity cost: because late males are, by definition, establishing their territories after other males have started breeding, late males miss opportunities both to engage in extra-pair copulations (as discussed earlier) and to fledge young early in the season in their first year. In female New Zealand stitchbirds (*Notiomystis cincta*), lower reproductive success of first-year females is nearly entirely because of timing of territorial establishment: nearly half of first-year females delay reproduction until after older birds had initiated breeding (Low et al. 2007). In our study, only two late-establishing males were able to successfully fledge young in their first

year during our observation period (i.e. before the end of June), although many did obtain females and may have fledged young later in the season. Overall, however, first-year males are less likely than older males to successfully fledge young in May or June (Hughes unpub. data), so the opportunity cost of missed nest attempts early in the first year on territory may not be high.

Thus, late territory establishment may allow males entering the population to reduce costs of territorial establishment without loss in territory tenure (Fig. 1); if late establishers are able to subsequently relocate their territories, they can obtain higher early season nesting success/year (Fig. 3). On the other hand, late establishment precludes early season nesting success (probably also extra-pair success) during a male's first year on territory and is only a successful territorial behavior if males are able to move to a new territory in subsequent years.

Site Fidelity

Although site fidelity is generally thought to increase with age in territorial birds (Greenwood & Harvey 1982), we found that relocation was independent of time on territory in our song sparrow population – territory relocation was not more common in younger or older (potentially senescing) males. Movers actually had longer tenure than site-faithful males (Fig. 1); this result could occur either because moving facilitates increased tenure or simply because the longer a male is on territory, the more opportunity he has to relocate. In either case, however, it is clear that low site fidelity does not reflect an overall inability to defend a territory.

Variation in site fidelity may be a facultative response to territory quality: in some species, male site fidelity is related to breeding success (Brooke 1979; Haas 1998; Hoover 2003). While moving appeared to be beneficial for late-establishing males, at least in terms of early season nesting success, early establishing males did not benefit from territory relocation (Fig. 3). Given that many late-establishing males appear to target territorial males with young, some early establishing males may be forced to move as a result of losing their territories while engaging in parental care: 26% of movers relocated the season following a successful previous season. Interestingly, all but one of the males who moved following a successful breeding season was in their first year on territory, and none of them successfully fledged another nest early in the season throughout the remainder of their tenure. These

birds were successful early in their first year of tenure, and moving appears to have resulted in a decrease in early season nesting success. In contrast, for birds whose territorial move did not follow a season with early nesting success, the average number of early season successful nests/year was nearly four times greater on their new territory. Thus, territorial relocation in male song sparrows may have two distinct causes: some males (particularly those who established their first territory late in the breeding season) move strategically to increase territory quality; other males (primarily those in their first year) lose their territories while investing in parental care and subsequently end up on lower quality territories. A larger sample size will be necessary to further explore whether the consequences of moving are different for different subsets of males.

Conclusion

In song sparrows at our site, individual variation in both time of first territory establishment and site fidelity appear to be important aspects of territorial behavior. In particular, late-establishing males who subsequently relocate their territories appear, by the measures used in this study, to do as well or better than the majority strategy of early establishment and site fidelity. The degree to which lifetime early season nesting success correlates with lifetime reproductive success, however, is not known. If late-establishing movers have higher lifetime reproductive success than males engaging in other territorial behaviors, the question of why only 10% of males engage in this combination of territorial behaviors remains. Alternatively, if the high success of late-establishing movers early in the season is offset by higher success of early establishing non-movers later in the season or in extra-pair behavior, then what we have discussed simply as territorial behaviors may be better viewed more broadly as alternative reproductive strategies. In either case, these results point to the importance of examining individual variation in territory defense behaviors.

While early territory establishment and high site fidelity are clearly the norm, behaviors such as late territory establishment and territory relocation cannot be dismissed as anomalous or indicative of low-quality individuals. These behaviors instead appear to be facultative alternatives for territorial defense, resulting in lifetime tenure and early season nesting success as high or higher than early establishing, site-faithful males. It is not always obvious which phenotypic variants may be important to under-

standing a system; the individual variation in territorial behavior explored here illustrates the importance of considering the functional significance of apparently abnormal behavioral variants.

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