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Individual variation in response to simulated territorial challenge among territory-holding song sparrows

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Lack (1946) suggested that male songbirds exhibit consistent individual differences in the vigor or manner in which they defend their territories against intrusion. The causes and consequences of such individual variation have not been incorporated into models of territoriality, however, because of a lack of experimental data confirming Lack's suggestion. In this paper, we test the possibility that male song sparrows *Melospiza melodia* who are successful territory holders differ consistently in the vigor with which they defend their territory, by conducting repeated song playback trials with the same set of territory-holding subjects across a breeding season. We found only relatively weak seasonal trends in responsiveness: the amount birds sang in response to playback increased significantly across the breeding season and responsiveness was generally lower when a male's social mate was egg laying. By contrast, we found extensive variation among males in how closely they approached a simulated territorial intrusion. These individual differences remained significantly consistent across four rounds of playback trials that spanned the breeding season as determined by Kendall's coefficient of concordance. Our results confirm that some individual song sparrows are consistently more vigorous than others in territory defense, at least in one conspicuous aspect of their behavior, and suggest that further work is needed to understand the nature and consequences of variation in patterns of defense among successful territory holders.

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In his classic study, *The Life of the Robin*, Lack (1946) observed that individual males differ dramatically in their response to territorial intrusion, as simulated by the presence of a mount: "A few ignored the stuffed bird altogether, some attacked only feebly and briefly, others for rather longer, and some violently" (p. 151). Lack went on to underscore the consistency with which different individuals used different tactics in territory defense: "If the specimen was shown to the same robin on a later occasion, it used the same method of attack and posturing as before, showing that such differences were characteristic for each individual" (p. 151). Since Lack's time, there has been considerable interest in the ecological correlates and evolutionary consequences of territoriality, leading to the general consensus that an animal will be territorial if the benefit of having exclusive access to some resource outweighs the cost of defending it (Brown 1964, Gill and Wolf 1975, Davies and Houston 1984, Maher and Lott 2000). The emphasis of this work, however, has been to ask whether an individual (or population or species) will be territorial or not; by contrast, there has been little discussion of the causes and consequences of individual differences in the strength or manner of territorial defense as described by Lack (but see Dabelsteen and McGregor 1996).

In our experimental playback studies of migratory song sparrows *Melospiza melodia* (e.g., Searcy et al. 1997, 1999), we have found that males vary greatly in their response to simulated territorial intrusion. Some

males sing at length, while others remain relatively quiet; some fly in an agitated fashion around the loudspeaker, at times landing on and pecking at it, while others remain at a distance even though it is clear they are aware of and responding to the playback stimulus. It is not surprising to observe variation in response to identical stimuli in playback experiments, given that many contextual factors have been shown to influence the strength or nature of an individual's response, including time of day, stage in the breeding cycle, relative position of the stimulus on the territory, and the presence or absence of mates or offspring (e.g., Ickes and Ficken 1970, Verner and Milligan 1971, Yasukawa 1978, Giraldeau and Ydenberg 1987, Falls 1992). Typically, experiments are designed to minimize this variation by controlling for such factors, but it is usually not possible in the field to control all factors that may have a short-term effect on male response. Nonetheless the striking variation we have observed led us to wonder if, as suggested by Lack, some individuals are consistently more vigorous in the defense of their territory while others are consistently less so, even in the face of other short-term factors affecting their response. In this paper, we address this question by conducting repeated playbacks with the same set of territory-holding subjects, asking whether the relative strength of individual responses remains consistent across a breeding season.

Consistent individual differences in territorial defense might arise due to individual variation in resource holding potential (RHP). *A priori* it seems logical that those males lowest in RHP would be the ones that would be least vigorous in defense. Yasukawa (1979), however, found that male red-winged blackbirds *Agelaius phoeniceus* that were successful in establishing territories were actually less vigorous in aggressive display than those that failed, suggesting that the males of highest RHP can retain their territories with little effort. Alternatively, consistent differences in how individuals defend their territories might correspond to individual variation, not in RHP, but in the relative cost/benefit ratio of territory defense (*sensu* Davies and Houston 1984). Less vigorous defenders may have a lower payoff from defending their territory because, for example, the quality of their mate or territory is low, or because they have incurred a high level of cuckoldry. A third possibility is that apparent differences in the vigor of territory defense reflect alternative, but equally successful defense tactics. By this view, males that appear to be less vigorous in our experiments may engage in other activities not elicited by simulated intrusion that help maintain their territories or otherwise enhance reproductive success.

As a first step towards addressing these issues, we conducted experiments designed to confirm or refute our impression that some male song sparrows are consistently more vigorous in territory defense than others. We first look to see if two primary behaviors associated with response to territorial challenge – approach and song – are correlated. If they are not correlated, then we have to consider the possibility that individuals show consistent differences in some aspects of territory defense but not in others. We next evaluate seasonal changes in response, because such changes may obscure individual consistency, especially since individuals are unlikely to be in exactly the same phase of their breeding cycles as our tests progress across the season. Finally, we use a test of concordance to determine whether there are consistent individual differences in response to simulated intrusion.

Materials and methods

Subjects were 12 male song sparrows holding territories in 1998 within an approximately 20 ha study area, located on State Game Lands 214 near Hartstown, Crawford County, Pennsylvania, USA. We marked all subjects with a unique combination of colored leg-rings for individual identification. Two of the subjects held adjacent territories, but in all other cases subjects were separated by at least one and usually several intervening territories. For eight of the subjects, we color-marked their neighbors and monitored breeding activity of those neighbors as well as the subjects throughout the season. The other four subjects held territories in areas that we monitored less intensely; these birds had unmarked neighbors.

We tested subjects with playback of song sparrow songs that had been recorded using either a Sony TC-D5M or a Sony TCM 5000EV tape recorder with a Shure SM57 or Realistic 331070B microphone in a Sony PBR-330 parabola. Recordings were made several years earlier from an area about 5 km distant from our study area. Thus, test stimuli were local songs but it is extremely unlikely that any of our subjects were familiar with the playback songs they heard or with the individuals that originally sang them. We chose songs to be used for playback based on quality and background noise level from among hundreds of songs that had been recorded from each source male, digitized these songs using "Signal" v 3.0 software (Engineering Design 1996, 16 bits, 25 kpts/s sample rate), and recorded playback tapes from these digital copies.

Playback tests involved broadcasting song sparrow song from near the center of the subject's territory for 6 min at a rate of 1 song/10 s, using a Sony TCM 5000EV tape recorder and an Acoustic Research "Powered Partner" speaker-amplifier, at an amplitude of 86 dB SPL (measured at 1 m). We determined territory boundaries by observing encounters between neighbors for several days before playback trials began, in a few cases provoking those encounters with playback of 2–3

songs at the point we thought a boundary occurred to confirm our estimate. Song sparrows in our population generally nest along the edges of fields and thus their territories are essentially linear, making it easy for us ensure that the loudspeaker was placed centrally on the territory. We marked the position of the loudspeaker with plastic flagging to ensure that its placement was identical in subsequent tests on the same territory. Each 6-min playback tape included 2 different song types recorded from the same source male presented in the order: 9 repetitions of the first type, 9 repetitions of the second type, 9 repetitions of the first, and 9 of the second. We made 12 different playback tapes, using 24 songs recorded from 6 different source males.

Two observers monitored the subject during tests, recording two response measures: the distance between the subject and the playback speaker ("distance to speaker") and the number of songs the subject sang. We confined our analysis to these two measures because they could be reliably recorded by observers standing at a distance (as compared to softer calls and visual displays such as crest raising); our previous work has demonstrated that the distance measure alone reliably captures even subtle differences in response to different stimulus categories (e.g., Searcy et al. 1997, 1999). Data were recorded during the 6 min of playback and for an additional 3 min after playback had concluded, for a total observation period of 9 min. Distance to speaker was sampled at 5-s intervals, binned into the categories 0–2 m, 2–4 m, 4–8 m, 8–16 m, and >16 m. Before playback began, markers were positioned at 4, 8 and 12 m relative to the loudspeaker to facilitate distance estimation. In calculating an average distance to the speaker, we considered a bird in the 0–2 m range for a given 5-s interval to be at 1 m from the speaker during that interval, a bird in the 2–4 m range at 3 m, in the 4–8 m range at 6 m, in the 8–16 m range at 12 m, and in the >16 m range to be at 24 m, following the method of Peters et al. (1980). The average distance was calculated from these 5-s interval estimates across the entire 9-min observation period. The number of songs produced was simply totaled across the 9-min observation period.

We tested each subject 4 times across the season; we refer to each set of tests as one "round" of testing. Individual tests within a round were spread over 2 or 3 consecutive days, with no individuals who were close enough to hear another test being tested on the same day; subsequent rounds were done at approximately 2 week intervals. Each of the 12 subjects heard a different playback tape within each round of testing, and individuals heard a different playback tape on each subsequent round.

Three of our subjects disappeared over the course of the season, one before Round 3 of testing and two others before Round 4. The first bird to disappear is known to have died in an accident unrelated to our work; we could not determine the fate of the other two birds, although our failure to find these birds after extensive searching for several days following the fourth round confirmed that they had disappeared permanently from their territories (as opposed to them being present but simply not responding to playback). Thus, our sample size is diminished to $N = 11$ for analyses involving the first three rounds and to $N = 9$ for analyses involving data from all four rounds. Aside from cases in which the subject had died or disappeared permanently, birds clearly responded to the playback stimulus in virtually all trials, even if their overall response was weak, as evidenced by approaching at least once to within 8 m of the speaker (and within 4 m in over 90% of trials). There were only two trials in which the subject never approached within 16 m. In both cases, however, these birds were observed singing on their territories shortly before the playback trial began and again within a few hours after the trial concluded, so we included data from these trials as minimal responses.

We base our statistical analyses on the subset of 9 birds for which we have data across all four rounds, but in some cases we also include analyses based on data from 11 birds across the first three rounds or all 12 birds across the first two rounds. In cases where we present multiple analyses using different sample sizes (i.e., $N = 9$ over 4 rounds vs. $N = 11$ over 3 rounds), we only provide a P value for one analysis, but provide information from the parallel analysis for heuristic purposes.

Results

When the data from 9 individuals are averaged over all four rounds, a significant correlation exists between the two response measures, distance to speaker and total number of songs (Fig. 1). This correlation is negative, but lower approach scores and higher song scores both correspond to a more vigorous response. Thus, birds that approached the playback speaker more closely generally sang more as well. A significant relationship also is observed if data from 11 birds are averaged over the first 3 rounds. The relationship between approach and singing is noisy, however, as illustrated by the standard error bars in Fig. 1.

We found only weak evidence for seasonal variation in response across the four rounds of testing (Fig. 2). This lack of variation is surprising given that our four rounds approximately spanned a time from the onset to the end of breeding in this population (M. Hughes, unpubl. data). Average distance to speaker appeared to increase between the first and last rounds, although the pattern was inconsistent and the differences were not statistically significant (Fig. 2A). The average number

of songs produced increased across the four rounds, with the difference between Rounds 1 and 4 being statistically significant (Fig. 2B). Note that the trends in approach and singing run contrary to each other in this analysis: larger average distances mean that the approach response diminished in strength through the season (although not significantly so), while the greater number of songs produced means the song response increased in strength.

Seasonal trends in responsiveness may be obscured in the above analysis because breeding is not highly synchronous in this song sparrow population (M. Hughes, unpubl. data). Thus, by averaging response by round (i.e., by absolute time across the season) we are likely to be averaging together data from birds in different stages of their breeding cycle. An interesting seasonal trend does emerge if data are grouped by breeding cycle stage instead of by round (Fig. 3). Specifically, response to playback decreased dramatically when the social mate of the test subject was egg-laying. The trend runs in the same direction for approach distance as for song, with increased distances and decreased number of songs both reflecting reduced response to playback. Note that the sample size in this analysis is too small to permit statistical analysis because we only had unambiguous information about breeding stage for a subset of playback trials.

We used Kendall's coefficient of concordance (Siegel 1956) to ask whether the relative ranking of individuals' responses remained consistent across successive rounds of testing. The concordance among distance to speaker scores for the 9 birds tested across all 4 rounds was significant ($W = 0.604$, $df = 8$, $P = 0.013$). Analysis of distances for the 11 birds tested across the first 3 rounds yields an even more robust result ($W = 0.757$, $df = 10$). The consistency of response revealed by the coefficient of concordance can be seen by plotting distance to speaker in the first round of testing against the response of these same individuals in second round (Fig. 4A).

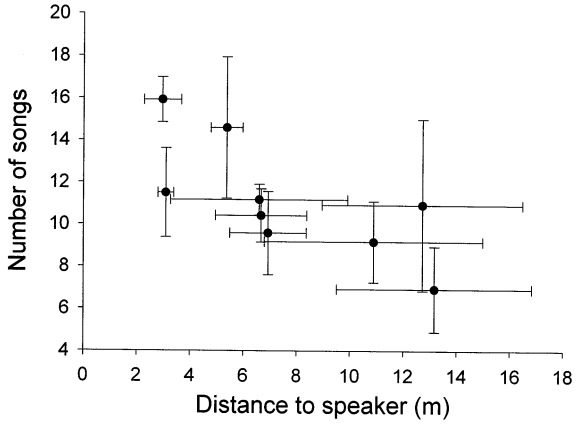

Fig. 1. Correlation between average distance to speaker and total number of songs recorded, for 9 individuals whose data have been averaged over all 4 rounds of testing. Means ± SE (for both response variables) are shown. Spearman rank correlation shows the relationship is significant ($r_s = -0.88$, $P < 0.01$).

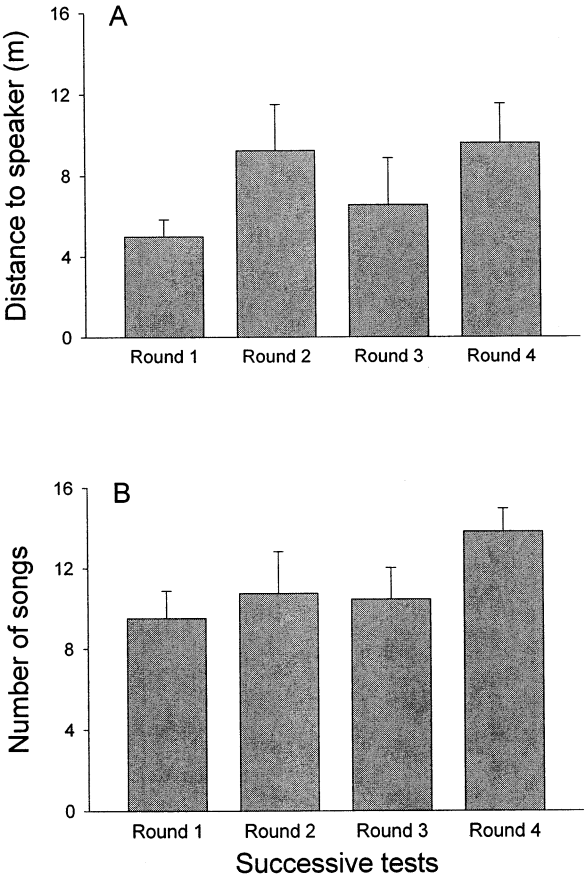

Fig. 2. (A) Distance to speaker and (B) number of songs averaged across subject for the four rounds of testing. The average distance to speaker does not differ significantly across test rounds (Friedman test statistic = 5.13, df = 3, P = 0.162). The average number of songs produced does differ significantly among test rounds (Friedman test statistic = 9.30, df = 3, P = 0.026); post-hoc testing (Conover 1980, p. 300) reveals that only Round 1 and Round 4 differ from each other significantly. Means ± SE are shown; N = 9 throughout.

Although we observed some consistency in the amount individuals sang across different rounds (Fig. 4B), the Kendall coefficient of concordance for this measure is not significant for the 9 birds tested across all 4 rounds ($W = 0.338$, $df = 8$, $P = 0.213$); the coefficient is greater if data from 11 birds tested across the first 3 rounds are analyzed ($W = 0.493$, $df = 10$) but also would not be significant.

Discussion

Differences among male song sparrows in how closely they approached a simulated territorial intrusion were significantly consistent across four rounds of playback

trials that spanned the breeding season (e.g., Fig. 4A). Thus, our results confirm our impression that some individuals are consistently more vigorous than others in territory defense, at least in one conspicuous aspect of their behavior. Although there was some consistency in differences among males in the amount they sang in response to playback (Fig. 4B), this trend was not statistically significant. In general, individuals who approached a presumed territorial challenge more closely also sang more in response to this challenge (Fig. 1); this relationship was noisy, however, possibly because there was a significant seasonal effect in how much males sang (Fig. 2B) which was not observed in how closely they approached the loudspeaker (Fig. 2A). We can conclude, then, that individual territorial male song

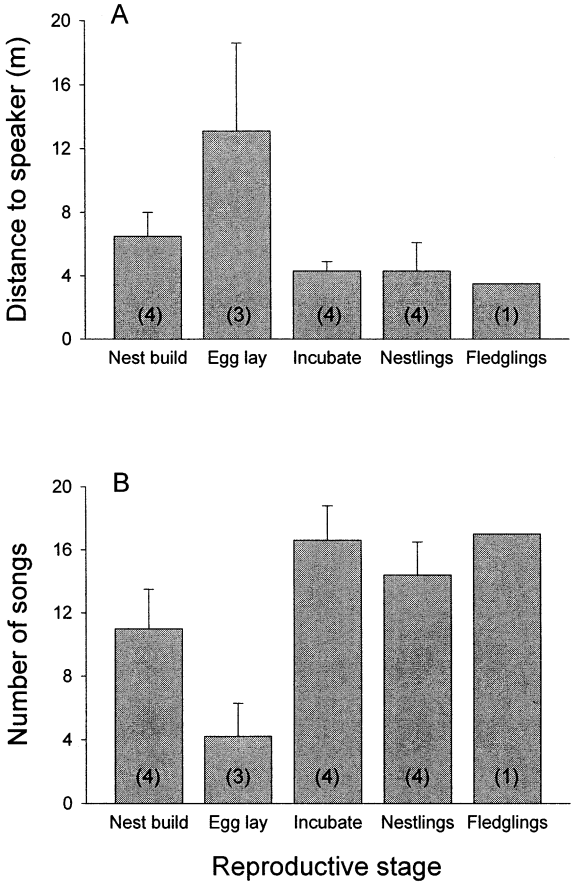

Fig. 3. (A) Distance to speaker and (B) number of songs averaged across individual by stage in the breeding cycle. We lumped data into five breeding cycle stages: nest building, egg laying, incubation, feeding nestlings and feeding fledglings. Note that the sample sizes are reduced because we only used data from trials where we had unambiguous information about breeding stage. Such information was only available from the 8 birds in our main study area and in several cases we could not determine with certainty the exact breeding stage on the day when a trial was performed. Means $\pm$ SE are shown, with sample sizes in parentheses. Sample sizes are too small to permit statistical analysis.

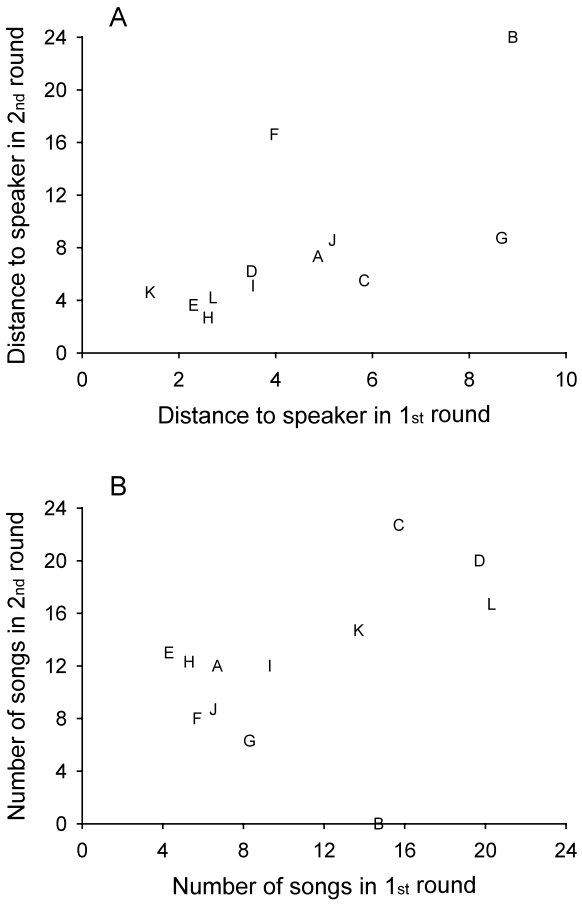

Fig. 4. (A) Distance to speaker and (B) number of songs for individuals in Round 2 as a function of distances in Round 1. Individual identities are indicated by letters to facilitate comparisons between plots. Birds D, E and L are the 3 individuals not included in the core sample of 9 used for statistical analysis (see text).

sparrows differ in the nature of their aggressive response, although our data fall short of supporting Lack's (1946) broader conclusion that individual males employed distinctly different suites of tactics in territorial defense.

We expected responsiveness to decrease significantly over the course of the breeding season, but this proved not to be the case. In fact, we observed just the opposite trend for song, with response increasing significantly from the beginning to the end of the season (Fig. 2B). The functional significance of this increase, if any, is unclear. The strongest seasonal trend we observed was a pronounced decrease in male response to playback when the social mate was egg-laying (Fig. 3). The biological significance of this trend needs to be interpreted with caution, because the sample size in this analysis was not sufficient for statistical analysis. Nonetheless, this result seems at first glance to be counter-intuitive: one might expect males to be more,

rather than less responsive to territorial intrusion when females are fertile and laying. A plausible explanation is that males with a fertile female on their territories tend to respond to playback by approaching and guarding their mate rather than by approaching the supposed intruder (e.g., Møller 1987).

In some species, whether or not an individual is territorial depends on the relative costs and benefits of defending a critical resource (Gill and Wolf 1975, Davies and Houston 1984). In species where economic defendability generally favors territoriality, however, whether or not a male possesses a territory usually is an overwhelming determinant of its reproductive success (e.g., Nolan 1978, Smith 1988, Searcy and Yasukawa 1995). Non-territorial males may achieve some reproductive success (Ewen et al. 1999, Kempenaers et al. 2001), but evidence suggests that territorial males in a population father most offspring, even those resulting from extra-pair fertilizations (Kempenaers et al. 2001). Thus, it is surprising to find that some individuals do not appear to devote as much effort as others to territorial defense, given its importance for reproductive success.

We have no evidence to suggest that the consistent differences we observed among males corresponded to intrinsic differences in competitive ability – that is, the ability to obtain and hold a territory – as described by Yasukawa (1979) for red-winged blackbirds. The 9 birds used in our statistical analysis all held their territories for the duration of the breeding season. Two birds in our initial sample of 12 disappeared before the final round of testing, but neither appears to have been ousted because they were unable to defend their territory. Neither territory was reoccupied by another bird (although a neighbor was observed to encroach on one territory after its owner disappeared) and both of these birds had response scores for the trials in which they participated that were equal to or more vigorous than (i.e., closer approach and more songs) the average responses of the 9 birds in our core sample. Further, all of the territories occupied by birds in our sample were more or less equivalent in size, habitat characteristics and number of neighbor territories. However, we cannot rule out the possibility that more subtle differences in territory quality, or differences in mate quality or mate fidelity, corresponded to the variation we observed among males. Such differences, in turn, may be explained by intrinsic differences among males in their competitive abilities, perhaps related to age, with less vigorous males obtaining poorer territories, incurring more cuckoldry, and so forth. Even if males are equivalent in their competitive abilities, other factors, such as time of return from migration, may lead to disparities in territory or mate quality that result in differences among individuals in the cost/benefit ratio for territory defense. In this case, differences among individuals in the vigor with which they defend a territory would not be the cause of, but instead the result of differences in the value of their territory or social mate.

Lack's (1946) description of individual variation in "method of attack or posturing" suggests he thought such differences might reflect alternative but equally successful tactics for territory defense. By this view, birds that respond weakly with respect to approaching a presumed intruder might respond strongly in some other component of territorial defense that we did not measure or that was not elicited by our test procedure. The overall correlation we observed between closeness of approach and amount of song provides some evidence against this view, but we cannot rule out this possibility without more extensive observation of birds' behavior in response to different kinds of territorial challenges. Another possibility is that variation in the strength of territorial response corresponds to alternative tactics for optimizing reproductive success. For example, less aggressive male yellow warblers *Dendroica petechia* expend more effort on parental care (Studd and Robertson 1988). We also are not able to determine whether this possibility holds for song sparrows in our population based on the present study. Our data do suggest, however, that further work is warranted on individual variation in territorial behavior, not simply in terms of whether or not an individual should defend a territory, but also on the nature and consequences of variation among successful territory holders.

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