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Territory switching behavior in a sedentary tropical passerine, the dusky antbird (*Cercomacra tyrannina*)

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Demographic data from an 8-year study of a marked population showed that switching territories and mates is common in both genders of dusky antbirds (*Cercomacra tyrannina*), a sedentary neotropical passerine with year-round territories and pairbonds. We conducted 22 experimental removals and followed six natural disappearances to examine territory switching. Antbirds quickly abandoned territories and mates to move to openings created by experimental removals. Pairing with the resident on a new territory was rapid. Unmated birds attracted new mates by singing a gender-specific song that differed from songs given by mated birds. There were no gender differences in replacement time or rate. Some vacancies, experimental and natural, were not filled, suggesting that floaters were rare. Territory and mate switching were not related to immediate enhancement of reproductive success because the probability of reproducing successfully was equally poor on all territories. Territory switching may be an overlooked but common tropical form of territoriality that increases individual survivorship during periods of low food abundance (dry season). We suggest that switching is favored when low annual reproductive success enhances selection for a long lifespan as the primary means to increase reproductive success. *Key words:* Aves (birds), removal experiments, RHP, territory switching, mate switching, mate choice, genetic monogamy, *Cercomacra tyrannina,* tropical passerine, antbird. *[Behav Ecol 11:648–653 (2000)]*

Year-round territoriality with permanent pairbonds is a common breeding system of tropical passerines but is nearly absent in temperate passerines. Many insectivorous tropical birds, 65% of passerine species in Panama (Morton, 1980), for example, have longstanding, nearly unchanging, territory boundaries and low turnover in adults. The stability (Greenberg and Gradwohl, 1986, 1997) that these characteristics provide to neighborhoods of conspecifics is unknown in temperate birds.

This tropical mating system, termed ''permanent monogamy'' by Freed (1987), is the most prevalent but least studied mating system among birds (Mock, 1985). Here we report an 8-year study of this system in a tropical passerine bird, the dusky antbird (*Cercomacra tyrannina*). Pairs appear to remain together and jointly defend territories year-round (Morton and Derrickson, 1996). With an annual survivorship of 0.82, which does not differ between genders (Morton and Stutchbury, in press), few vacancies due to deaths would be expected (Ashmole, 1963; Ricklefs, 1980). Under these conditions, floaters are expected (Smith, 1978) and male and female vacancies should be filled equally rapidly.

Few studies have examined pair stability in tropical birds, where the constraints on mate choice and territory switching are vastly different than for long-distance migrants that breed in the temperate zone. Freed (1987) documented long-term pairbonds, generally for life, in tropical house wrens (*Troglodytes aedon*). He showed that these long-term pairbonds result from constraints rather than any direct reproductive advantages. Furthermore, removal experiments have rarely been done in tropical birds (e.g., Levin, 1996; Morton, 1977). Removals in temperate zone studies generally show that floaters (previously non-territorial) replace removed individuals (e.g., Smith, 1987; Zack and Stutchbury, 1992). Often replacement birds are of younger age or lower quality (Hogstad, 1989; Mönkkönen, 1990; Sherry and Holmes, 1989). Beletsky (1996) summarizes extensive removal experiments in red-winged blackbirds (*Agelaius phoeniceus*) designed to study territorial acquisition and retention.

We studied territory acquisition and the stability of pair bonds by conducting removal experiments and tracking a colorbanded population of dusky antbirds. We determined that territory and mate switching is common and examined a series of questions concerning the evolution of territory switching. Do replacement mates come from a non-territorial floater population or do territory owners abandon current territories and mates to become replacement mates? Does one gender leave territories more than the other does? What qualities of territories make them attractive or unattractive to potential replacement birds? Are territories limited? Do territory boundaries change when replacement or removal occurs, how long does it take for a removed bird to be replaced and are there gender difference in the likelihood of being replaced? We discuss these questions in relation to the evolution of territory switching as a potentially widespread life history trait in tropical birds.

METHODS

Study site

Our study took place during 1991–1998 in central Panama in the Parque Nacional Soberania near Gamboa along the Pipeline Road and in Gamboa. The region is covered with mesic tropical forest and has abundant forest edge habitat used by dusky antbirds. There are distinct wet (May–December) and

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dry (January–April) seasons. We logged 16.7 dry season months and 4.8 wet season months in the field during these years. We studied breeding season behavior in the early rainy season, May–July in 1994 and 1995 (see Fleischer et al., 1997). Data presented here were obtained mostly in the dry season, when the birds do not breed.

We captured, measured, and colorbanded dusky antbirds occupying from 14, at the start of the project in 1991, to 50 territories in 1996. We captured pairs in a single mist net set up over a speaker playing back pair duets (see Morton and Derrickson, 1996). Once one or both adults on a territory were banded, that territory was visited each year 10–30 times and replacement individuals captured and colorbanded. Demographic data are presented elsewhere (Morton and Stutchbury, 2000).

Study species

Dusky antbirds are members of the suboscine passerine family Thamnophilidae, a species-rich neotropical group (Sibley and Monroe, 1990). Pairs defend territories year-round in brushy forest edge habitat where they forage 0.5–10 m up in vines, and vine-covered tree branches, shrubs, and grass. Nests are small (ca 23 cm long) bags made of black rhizomorphs (fungal ''horsehair''), suspended 1–4 m above the ground from the end of vertical vines or bamboo shoots (*Chusquea* spp.), always well-shaded and isolated from surrounding vegetation (and climbing predators) by 1–2 m. These nest site requirements are not uncommon but are fulfilled only by shade produced by forest trees, and not the shrubs and grass used for foraging. Dusky antbirds, therefore, are restricted to forest edge and gap habitat (Williams-Linera, 1990). Birds glean invertebrates from bark and leaf surfaces, hopping along branches and making quick dashes or brief hovers, and also poke into, and tap with their beaks, curled leaves or dead leaves caught in vines.

Males and females differ in plumage and song, produced in duets or separately (Morton and Derrickson, 1996). Males weigh 16.0 g (n = 18) and females 15.2 g (n = 11). Males retain a female-like plumage (brownish rusty-orange below, olive-brown above) until one year of age, when they attain the dark grayish adult male coloration. During this juvenal plumage, males can be identified in the field by their use of the male song. Eye color allows aging of both genders up to 3 years of age (Morton and Stutchbury, 2000). Dusky antbirds neither join in mixed species flocks nor regularly pursue prey displaced by army ants (Willis, 1985). They defend territories vigorously at all times of year (Morton and Derrickson, 1996). Special gender-specific courtship songs function to attract a new mate (Morton, 1996). Dusky antbirds are socially and genetically monogamous (Fleischer et al., 1997).

Removal experiments

From 1991 to 1995 we removed 12 male and 10 female antbirds from their territories. We always left one member of the pair on the territory from which a removal was made. Also, we observed natural disappearances of two females and four males from their territories. Birds were captured in mist nets and transported in paper bags to holding cages. They were provided with mealworms and water ad libitum and kept individually in small (46 × 46 × 46 cm) hardware cloth cages covered with plastic camouflage mesh, to mimic a dense vine habitat, and kept in a room with ambient light and temperature for from 12 to 216 h. Birds were weighed when captured and when released back on their territories. This procedure worked well for this species, which has never before been kept in captivity, and we lost no individuals.

The removal experiments provided us the opportunity to monitor replacement behavior. We monitored the territory for replacement birds for the first 2 h after a removal and thereafter every 2 to 4 h. The bird still on the territory began singing a distinctive ''courtship'' song within 5 min of the removal (Morton, 1996). We used the presence of this courtship song to determine whether a replacement mate had arrived. The occurrence of duets indicated a replacement was consorting with the bird remaining on the territory. We played back duet songs to draw birds within view to either confirm the absence of replacements or to check for colorbands on replacements (Morton and Derrickson, 1996). We called new birds on the territory ''replacements'' when they were the same gender as the removed bird and when they sang duets with, and remained close to, the mates of the removed birds.

The original territory owner was released on the territory after a replacement had settled. Replacement time refers to the number of h between a replacement's arrival and the owner's release whereas ''time to be replaced'' is the number of h between the owner's removal and the arrival of a replacement. After one observer had the replacement in view, birds held in captivity were released back on their territories at the point of capture. A second observer monitored the released bird and recorded observations on the movements and behavior of the birds until one bird left the territory.

Natural disappearances were ascertained by the appearance of the courtship song and confirmed when only single, formerly paired birds, responded to duet playbacks. These territories were monitored 3–4 times per week for replacements.

Quality of territories

We compared the territories birds abandoned and those moved to in several ways. Because song output may be directly related to territory quality in many species (e.g., Morton, 1986), we counted the number of songs by males and females and the number of duet songs delivered during the dawn chorus on these territories during 10 mornings in February and March 1994. Dusky antbird dawnsinging lasted about 1 h, beginning about 0615 h and ending by 0730h.

We also measured territory area and estimated the amount of foraging substrate it contained. To measure territorial boundaries, we mapped the singing and foraging locations of pairs. We also used playbacks to elicit territorial defense movements, noting where pairs stopped advancing towards the playback speaker. Foraging substrate volume for each territory was estimated as the number of m^3 of vines, shrubs, grass, and vine-covered tree branches from 0.5 to 10 m above the ground at the edge of the forest (Williams-Linera, 1990).

RESULTS

Removal experiments

Males and females were replaced with equal frequency and as rapidly. Of 16 males (12 removed and four natural disappearances), nine were replaced and seven were never replaced. Of 12 females (10 removed and two natural disappearances), five were replaced and seven were never replaced. This difference was not significant (Fisher's exact test, $\chi^2 = 1.266$, $p < .44$). Neither was there a gender difference in the time between removal of owners and arrival of replacements, comparing only owners that were replaced (Mann-Whitney U test, $U = 17.5$, $p = .71$). For nine males replacement took 9.6 ± 2.90 (SE) h and for five females replacement took 12.6 ± 3.03 h (Figure 1).

Most replacements were colorbanded birds (six of nine

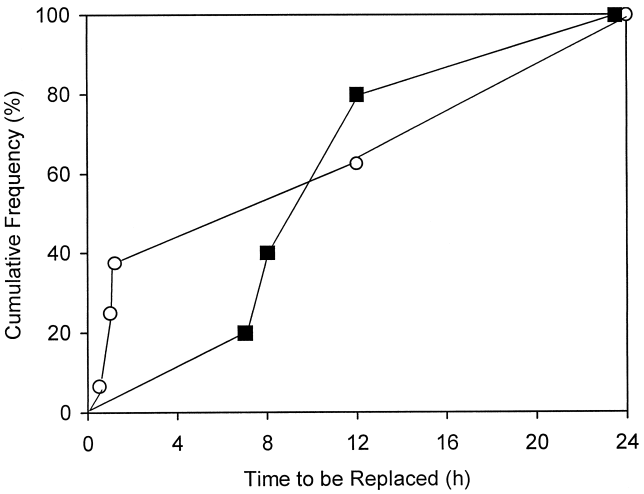


Figure 1
Cumulative frequency plot of time to be replaced for males ($n = 9$, circles) and females ($n = 5$, squares) experimentally removed from territories.

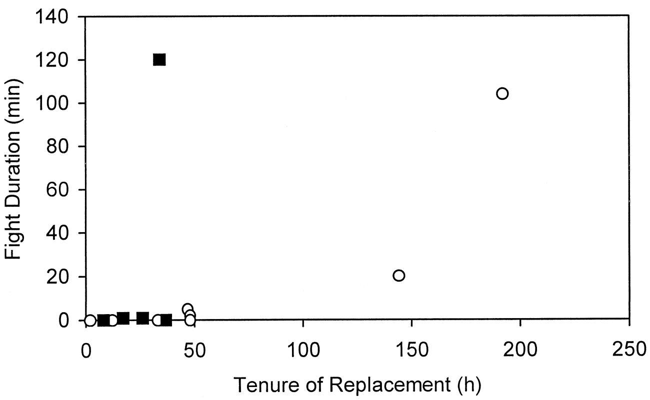


Figure 2
Duration of fights between replacement and released owner in relation to time replacement was on territory during owner's absence. One male was omitted because he did not regain his territory from the replacement. Males, circles; females, squares.

males and three of five female replacements) that left territories and mates to replace removed birds. The unbanded replacement birds also may have been territory-holders, rather than floaters, because all were in adult plumage. Furthermore, 43% (12 of 28) of the vacancies created by this territory switching remained unfilled, suggesting that floaters were rare.

Owners won back their territories regardless of when we removed them or the tenure of their replacements, with one exception. One male, after 48 h off territory, was unable to regain his territory from a replacement, which had been on the territory for 47 h. Instead, he moved to his replacement's former territory, which was adjacent to his original territory. He had lost 2.9 g in captivity, 18% of his weight at capture. This weight loss, the greatest experienced by any removed bird, was caused by unusually stressful housing (due to circumstances beyond our control).

When birds were removed for 48 h or less, little fighting occurred between the released owner and the replacement. The released owner threatened the replacement by exposing a white backspot (see Morton and Derrickson, 1996), and replacements fled. Some chases occurred, but no fights. After longer periods of residency, replacements confronted released owners and fought. Birds grappled and fell, fighting, to the ground, where we could see and hear them flapping and pecking one another in the leaf litter. We never observed such fights to occur naturally. The duration of chasing and fighting between the released owner and the replacement depended on the tenure of the replacement birds on the territory (Figure 2; ANOVA, $F_{1,11} = 4.315$, $p = .06$). One female/female confrontation lasted for 120 min despite a relatively short tenure by the replacement (Figure 2). If this outlier is removed, the relationship between fight duration and tenure becomes highly significant ($F_{1,10} = 30.253$, $p = .0003$).

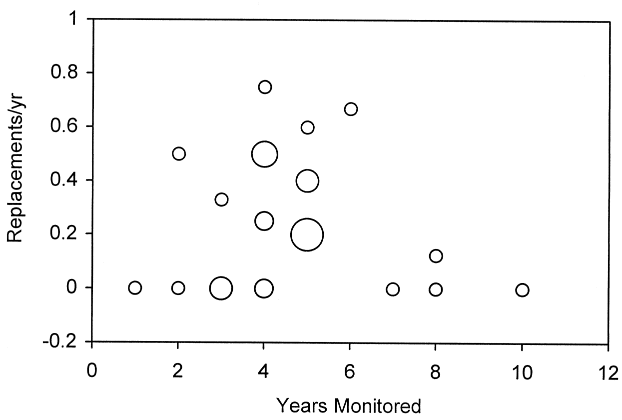
Non-experimental mate and territory switches

How common is mate and territory switching under natural conditions on unmanipulated territories? As our data are based on annual surveys and not continuous monitoring, they are minimum estimates of turnover rates. Also, we can not differentiate between death and emigration of occupants in many cases. Overall, we monitored 35 male changes on 32 territories for 143 territory-years (0.25 terr yr^{-1}) and 21 female changes on 24 territories for 93 territory-years (0.23 terr yr^{-1}). The difference in sample sizes is due to the fact that we were unable to capture females on some territories, despite repeated attempts, because males respond to song playbacks more quickly than females, often hitting the mist net first (Morton and Derrickson, 1996).

A bird may disappear from a territory because it died or because it emigrated. We estimated the rate of disappearance due to emigration alone by comparing the number of occupant disappearances with number of birds that were known to have emigrated because they were found living on another territory. In 16 adjacent territories, where nearly all birds were banded, 34 birds disappeared during 8 years. Sixteen of these birds (47%) were later found to be living on another territory. This (0.27 terr^{-1} yr^{-1}) is a minimal estimate of disappearance due to emigration because birds that moved out of the study area would be missed. We conclude that territory switches, or emigration, occurs commonly under natural conditions.

The replacement rate varied greatly among territories (Figure 3). Some territories had no changes for many years whereas others approached one change in occupant per year. There was a significant correlation between male and female replacement rates on territories ($r_s = 0.47$, $p = .04$, $n = 13$) monitored from 3–6 years. This suggests that males and females valued territories in the same way, and left or remained with equal likelihood when an opening occurred. Pair-members moved independently of one another. On only one occasion did we document a pair of birds moving together to a new territory. This move was to an adjacent territory where both male and female owners had disappeared. When their replacements on their former territory were removed they remained on their new territory, suggesting that their move was voluntary.

Some individuals lived on the same territory for many years, suggesting they valued these territories highly. Did these territories increase longevity? To examine this question, we looked at the age of the mates of birds that did not emigrate. Our expectation was that, if the territory was of high quality (in terms of survival), their mates should also remain on the territory and live longer than average. There is no gender difference in survival so we compared longevity in these mates with longevity in the general population. The mean lifespan of these mates was 5.9 years ± 0.404(SE) ($n = 7$) whereas the mean lifespan of the general population was 4.9 years ± 0.259 ($n = 49$). Although in the direction predicted, this difference was not significant (Mann-Whitney *U* test, $U = 111.5$, $p = .14$).


a) Males

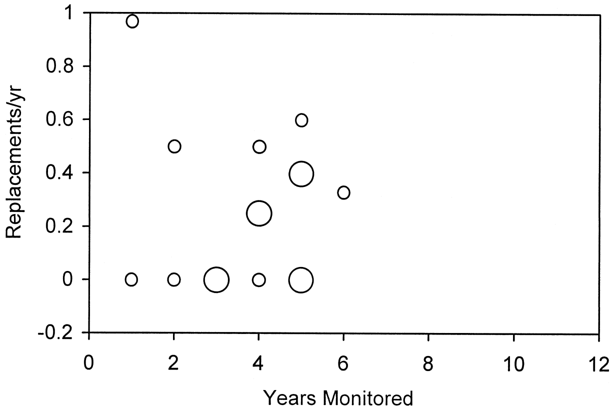

b) Females

Figure 3
The relationship between years a dusky antbird territory was monitored and natural replacement rate of male and female occupants. Bubble size indicates number of observations, ranging from 1–6.

Territory quality

Territories that were immigrated to tended to have more foraging substrate volume, but not necessarily more total area, than the territories from which the same birds emigrated (Table 1). No birds voluntarily moved to territories with less area or foraging substrate than their prior territory.

We focused attention on song output at three sites containing favored (removed birds replaced) and not favored (removed birds not replaced) adjacent territories (Table 2). There was no clear difference in song output on favored and unfavored territories (Wilcoxon, $n = 6$, $z = 0.52$, $p = .60$ for males; $n = 6$, $z = 0.11$, $p = .91$ for females).

Territories were not enlarged nor did their occupants change their boundaries over our 8 year study. Territorial boundaries remained the same on 36 territories that were occupied continuously during the study, even with turnover of individuals occupying them. The few territories that lost both occupants ($n = 4$) were not annexed by pairs of antbirds in adjacent territories. Thus, dusky antbirds apparently do not expand territories when the opportunity to do so exists.

Two territories were abandoned by antbirds when they were reduced. On one, ≈ 30% of the habitat was bulldozed, and on the other after underbrush was cleared. A pair of antbirds resettled in the first territory, which was vacant from January, 1992, until March, 1993, after the vegetation recovered; the second was not reoccupied.

Table 1
The size and foraging substrate volume of the territory moved to, in relation to the territory left

Foraging substrate	Territory area			
	Larger	Same	Smaller	Total
Larger	3	4	0	7
Same	0	1	0	1
Smaller	0	0	0	0
Total	3	5	0	8

DISCUSSION

Our results describe a mating system in which the individuals are always paired but readily abandon a territory to move to a better one. On some territories, birds left at the rate of one per two years (Figure 3). The territory switching system is characterized by gender equality, with both males and females capable of defending territories alone after mate desertion and attracting mates. Males and females were equally likely to leave territories and mates and did so independently, not as pairs. Thus mate abandonment is an important aspect of territory switching and, as a consequence, the evolution of cooperation between pair members is unlikely because the benefits of switching must be greater than those attained by maintaining long-term pairbonds. Indeed, we found no evidence of pair cooperation in territorial defense (Morton and Derrickson, 1996; see also Freed, 1987).

We suspect that intensive study of banded populations will find that territory switching is common and that stable pairbonding in tropical species with year-round territoriality is more apparent than real. Willis (1974) describes switching territories in the spotted antbird (*Hylophylax naevioides*), with females twice as likely to move as males. As with dusky antbirds, spotted antbirds moved to vacancies; they did not defeat owners. Checker-throated antwrens (*Myrmotherula fulviventris*) also switch territories, with 37% of adults, regardless of age and sex, moving to neighboring territories at least once in their lives (Greenberg and Gradwohl, 1997). More studies using removals are needed to document territory switching and mate replacement tactics in tropical birds.

We infer that floaters are uncommon in antbirds. Forty-three percent of territories (12 out of 28) remained unoccupied when their occupants disappeared naturally or due to our removal experiments (43% of vacancies). Most replacements were birds that switched territories rather than previously non-territorial birds. Furthermore, during the entire 8 year study, antbird pairs disappeared from 10 territories and

Table 2
Singing rate (number of songs per min) of dusky antbirds during dawnsinging, comparing 6 pairs of adjacent favored and not favored territories

	Males		Females	
Pair no.	Not favored	Favored	Not favored	Favored
1	1.71	2.32	0.30	0.23
2	1.71	1.31	0.30	0.31
3	1.87	1.45	0.72	0.28
4	1.16	6.06	0.73	3.95
5	1.16	3.48	0.73	1.24
6	3.80	1.31	1.70	0.31
Mean (SE)	1.90 (0.50)	2.66 (0.76)	0.75 (0.21)	0.90 (0.43)

were not replaced. The only new territories ($n = 4$) were established by juveniles, in pairs.

These data suggest that dusky antbirds are not limited by availability of territories. The data do not support the Ashmole/Ricklefs hypothesis that low adult mortality could influence reproductive rate through a density-dependent effect on food supply (Ricklefs, 2000). While population size may be stable (Greenberg and Gradwohl, 1986) this does not necessarily mean recruitment opportunities are low because carrying capacity has been reached (Ashmole, 1963; Cody, 1971; Ricklefs, 1980; Slagsvold, 1980). Adult survivorship was high (82%) but the likelihood that a pair raised young to independence averaged only 8% per year in our population (Morton and Stutchbury, in press). High quality territories, however, may be limited and most birds switch to get higher quality territories that enhance longevity.

New territories are established rarely, even in good dusky antbird habitat. The reason may be that territory establishment is constrained by predation (Lima, 1998). Dusky antbirds forage in dense habitat and do not have the predator-detection advantage gained by membership in interspecific flocks (Morse, 1977; Munn and Terborgh, 1979; Powell, 1985; Terborgh, 1990). Accordingly, birds switched territories only when a mate with experience on that territory was there, as evidenced by its special courtship songs.

A tropical/temperate difference concerned the frequency of removed owners regaining their territories from replacements. Temperate zone removals show that the probability that replacements will defeat the former resident increases with replacement time (Beletsky, 1996; Krebs, 1982). This is often a matter of only a day or two. These territories are used only for breeding. In contrast, dusky antbirds regained their yearlong territories regardless of replacement time up to 10 days, even though replacements fought longer after they occupied a territory more than 48 h (Figure 2). Perhaps released owners won because replacements could, and did, return to the territory they emigrated from and oust their replacements, if any. Removed residents, in contrast, did not have such an alternative to move to. The released owners' motivation to fight may have been higher than their replacements' motivation due to this asymmetry.

Birds cannot leave their current territories to assess other territories by exploring them (Morton and Derrickson, 1996). Nonetheless, birds appeared to switch to territories that had more foraging substrate though not always to larger ones (Table 1). We found no support for the idea that song output during the dawn chorus might affect decisions to switch (Table 2).

Further work on territory switching should focus on other factors. We do not know if the quality of a mate affects territory switching. Some pairs remained together on the same territory for long periods of time, even when experimental removals provided opportunities to switch, whereas other pairs broke up often. Reproductive success, however, was so low (8% per year) that no territory had more than one successful nest and many had no reproductive success during the 8 years of the study (Morton and Stutchbury, in press). Switching territories did not enhance annual reproductive success. Territory switching may evolve when successful reproduction occurs rarely in an individual's lifetime. Under this condition, selection favors a long reproductive lifespan as the primary means to achieve any reproductive success.

Longevity would be enhanced if birds switched to territories better for surviving periods of low food availability. Our study took place during the dry season, when insect abundance is lowest (Janzen, 1973; Janzen and Schoener, 1968; Wolda, 1978). Dusky antbirds may experience food stress during the dry season months and, as evidence of this, are missing from what appears to be excellent habitat on the drier parts of the Pacific coast of Panama only 15 km from our study site. Territory switches clearly were related to food resources in lesser sheathbills (*Chionis minor*) (Bried and Jouventin, 1998). The reasons for such switches are less obvious in dusky antbirds. Perhaps birds are able to judge, through their own foraging success on their current territories, how much of a gamble it would be to switch to another territory when a vacancy arises?

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REFERENCES

Ashmole NP, 1963. The regulation of numbers of tropical oceanic birds. Ibis 103:458–473.

Beletsky L, 1996. The red-winged blackbird, the biology of a strongly polygynous songbird. San Diego: Academic Press.

Bried J, Jouventin P, 1998. Why do lesser sheathbills *Chionis minor* switch territory? J Avian Biol 29:257–265.

Cody ML, 1971. Ecological aspects of reproduction. Avian Biol 1:461–512.

Fleischer RC, Tarr CL, Morton ES, Sangmeister A, Derrickson KC, 1997. Mating system of the dusky antbird, a tropical passerine, as assessed by DNA fingerprinting. Condor 99:512–514.

Freed LA, 1987. The long-term pair bond of tropical house wrens: advantage or constraint? Am Nat 130:507–525.

Greenberg R, Gradwohl J, 1986. Stable territories and constant densities in tropical forest insectivorous birds. Oecologia 69:618–625.

Greenberg R, Gradwohl J, 1997. Territoriality, adult survival, and dispersal in the checker-throated antwren in Panama. J Avian Biol 28: 103–110.

Hogstad O, 1989. The presence of non-territorial males in Willow Warbler *Phylloscopus trochilus* populations—a removal study. Ibis 131:263–267.

Janzen DH, 1973. Sweep samples of tropical foliage insects: effects of season, vegetation types, elevation, time of day, and insularity. Ecology 54:687–708.

Janzen DH, Schoener TW, 1968. Differences in insect abundance diversity between wetter and drier sites during a tropical dry season. Ecology 49:96–110.

Krebs JR, 1982. Territorial defense in the great tit (Parus major): do residents always win? Behav Ecol Sociobiol 11:185–194.

Levin RN, 1996. Song behavior and reproductive strategies in a duetting wren, *Thryothorus nigricapillus*: I. Removal experiment. Anim Behav 52:1093–1106.

Lima SL, 1998. Stress and decision making under the risk of predation: recent developments from behavioral, reproductive, and ecological perspectives. Adv Stud Behav 27:215–290.

Mock DW, 1985. An introduction to the neglected mating system. In: Avian Monogamy. Ornithological Monograph 37 (Gowaty PA, Mock DW, eds). Washington, DC: American Ornithologists' Union; 1–10.

Mönkkönen M, 1990. Removal of territory holders causes influx of small-sized intruders in passerine bird communities in northern Finland. Oikos 57:281–288.

Morse DH, 1977. Feeding behavior and predator avoidance in heterospecific groups. BioScience 27:332–339.

Morton ES, 1977. Intratropical migration in the Yellow-green Vireo and Piratic Flycatcher. Auk 94:97–106.

Morton ES, 1980. The ecological background for the evolution of vocal sounds used in close range. In: Acta XVII Congressus Internationalis Ornithologici, vol. 1(Nohring R, ed.). Berlin: Deutsche Ornithologen-Gesellschaft; 183–212.

Morton ES, 1986. Predictions from the ranging hypothesis for the evolution of long distance signals in birds. Behaviour 99:65–86.

Morton ES, 1996. A comparison of vocal behavior among tropical and temperate zone birds. In: Ecology and evolution of acoustic communication in birds (Kroodsma DE, Miller EH, eds). Ithaca: Cornell University Press; 258–268.

Morton ES, Derricson KC, 1996. Song ranging by the dusky antbird, *Cercomacra tyrannina*: ranging without song learning. Behav Ecol Sociobiol 39:195–201.

Morton ES, Stutchbury BJM, in press. Demography and reproductive success in the dusky antbird, a sedentary tropical passerine. J Field Ornithol.

Munn CA, Terborgh JW, 1979. Multispecies territoriality in neotropical foraging flocks. Condor 81:338–347.

Powell GVN, 1985. Sociobiology and adaptive significance of interspecific foraging flocks in the neotropics. In: Neotropical ornithology. Ornithological Monographs 36 (Buckley PA, Foster MS, Morton ES, Ridgely RS, Buckley FG, eds). Washington: American Ornithologists' Union; 713–732.

Ricklefs RE, 1980. Geographical variation in clutch size among passerine birds: Ashmole's hypothesis. Auk 97:38–49.

Ricklefs RE, 2000. Density dependence, evolutionary optimization, and the diversification of avian life histories. Condor 102:9–22.

Sherry T, Holmes RT, 1989. Age-specific social dominance affects habitat use by breeding American redstarts (*Setophaga ruticilla*): a removal experiment. Behav Ecol Sociobiol 25:327–333.

Sibley CG, Monroe BL, 1990. Distribution and taxonomy of birds of the world. New Haven, CT: Yale University Press.

Slagsvold T, 1980. Clutch size and population stability in birds: a test of hypotheses. Oecologia 49:213–217.

Smith SM, 1978. The ''underworld'' in a territorial sparrow: adaptive strategy for floaters. Am Nat 112:571–582.

Smith SM, 1987. Responses of floaters to removal experiments on wintering chickadees. Behav Ecol Sociobiol 20:363–367.

Terborgh J, 1990. Mixed flocks and polyspecific associations: costs and benefits of mixed groups to birds and monkeys. Am J Primatol 21: 87–100.

Williams-Linera G, 1990. Vegetation structure and environmental conditions of forest edges in Panama. J Ecol 78:356–373.

Willis EO, 1974. Populations and local extinctions of birds on Barro Colorado Island, Panamá. Ecol Monogr 44:153–169.

Willis EO, 1985. *Cercomacra* and related antbirds (Aves, Formicariidae) as army ant followers. Rev Bras Zool 2:427–432.

Wolda H, 1978. Fluctuations in abundance of tropical insects. Am Nat 112:1017–1045.

Zack S, Stutchbury BJ, 1992. Delayed breeding in avian social systems: the role of territory quality and ''floater'' tactics. Behaviour 123: 194–219.