

Experimental evidence that bright coloration is not important for territory defense in purple martins

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Summary. I tested the hypothesis that bright breeding plumage in territorial males acts as a badge of fighting ability or aggressive motivation to intimidate intruders. Territorial male purple martins (*Progne subis*) whose iridescent blue plumage was lightened to mimic the appearance of subadult males did not suffer an increase in intruder pressure or loss of territory compared with control males. Bright plumage color itself did not deter intruders and was not important for successful territory defense. Furthermore, a bright coloration of owners was not associated with an increased level of aggression toward intruders. Results from parallel studies on this species suggest that bright coloration is important in territory acquisition. The effectiveness of badges of fighting ability and aggressive motivation in territory defense is limited by whether intruders benefit from assessing these traits in owners. Differences in signaling systems between species are due in part to differences in floater tactics and the mode of territory acquisition.

Introduction

Plumage coloration plays a key role in avian communication, including individual recognition (Shields 1977; Whitfield 1986), intraspecific competition (Rohwer 1975; Rohwer et al. 1980; Hamilton and Zuk 1982), and possibly signaling to predators (Baker and Parker 1979; Flood 1989). Surprisingly, empirical studies testing hypotheses for the adaptive significance of plumage color patterns within and between species are seriously lacking in many areas (reviewed in Butcher and Rohwer 1989). Generally, in dimorphic species males are brighter than females, old birds are brighter than young birds, and breeding plumages are brighter than non-breeding plumages (Butcher and Rohwer 1989). This strongly suggests that bright coloration is a sexually selected trait.

Many studies have demonstrated a correlation between plumage brightness and mating success (e.g., Lifjeld and Slagsvold 1988; Payne et al. 1988; Norris 1990) or territory quality (e.g., Flood 1984; Studd and Robertson 1985a; Hill 1988). However, relatively few studies have tested whether manipulating a male's breeding coloration directly affects his competitive ability (Peek 1972; Smith 1972; Rohwer and Roskaft 1989; Hoglund et al. 1990) or mating success (Collias et al. 1979; Alatalo et al. 1990; Hill 1990). Plumage manipulations are essential for controlling other factors that may be correlated with bright coloration (e.g., age, size, vocalizations) and for demonstrating that plumage color itself serves a direct role in communication and functions as a signal (Butcher and Rohwer 1989; Rohwer and Roskaft 1989).

Rohwer (1982) proposed that conspicuous plumage coloration of breeding males evolves as a badge of fighting ability so that territory owners who are good fighters will be remembered by intruders, thereby deterring intruders from returning or escalating contests. A reduced intruder pressure would reduce the costs of territorial defense (energy, risk of injury) to the owner and perhaps allow more in time for other activities (e.g., feeding, courtship). This benefit of conspicuous coloration would be important for species in which there are repeated contests between the same individuals, many different individuals are involved in direct competition so that individual recognition is difficult, and fighting is risky so intruders will be selective of whom they challenge (Rohwer 1982; Rohwer and Roskaft 1989).

A critical prediction of the hypothesis that bright plumage signals good fighting ability (Rohwer 1982) or aggressive motivation (Studd and Robertson 1985b) is that territorial males whose bright badge is removed should suffer an increase in intruder pressure and be more likely to lose all or part of their territory to other males. In this study, I test whether the bright plumage of territorial purple martins (*Progne subis*) intimidates intruders by manipulating the plumage color of territory owners to mimic the appearance of subadult males. Adult male purple martins have a solid iridescent blue

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plumage, in contrast to 1-year-old males that have white undersides with varying amounts of iridescent blue (Niles 1972). In this study, males were manipulated within the natural range of plumage color variation, unlike similar experiments on other species (Peek 1972; Smith 1972; Rohwer and Roskoff 1989). Purple martins are colonial secondary cavity nesters (Allen and Nice 1952) and defend territories that consist of one or more nesting cavities and adjacent perch sites. During territory establishment, intrusion rates by males are high, and fighting is common, as individuals compete intensely for nesting cavities (Brown 1979; Stutchbury 1991b). Subadult male martins often obtain territories and breed (Morton et al. 1990, this study), so intruders normally encounter both adult and subadult male territory owners.

If intruders are intimidated by males with bright badges, then it is predicted that intruding males are less likely to escalate contests when intruding on territories of adult than subadult males. In order for bright coloration to intimidate intruders, the badge must be a reliable signal of fighting ability and aggressive motivation. Therefore, bright owners are predicted to be more aggressive in territory defense than are dull owners (Studd and Robertson 1985b). I tested these predictions by observing intrusions of nonterritorial male floaters on the territories of adult and subadult territory owners.

Methods

Populations of purple martins in eastern North America breed almost exclusively in nest-houses (Allen and Nice 1952). Historical records of large colonies in natural cavities and similarities in breeding behavior with a natural population in Arizona suggest that nest-houses adequately mimic natural conditions (Stutchbury 1991a). This study was conducted at two martin colonies nesting in houses. The colony at the University of Oklahoma Biological Station (UOBS) in Marshall Co., Oklahoma, was established around 1980, and typically has 40–50 pairs breeding in 6 nest-houses with a total of 72 compartments. The colony located in Sherman, Grayson Co., Texas, 50 km southeast of UOBS, typically has 20 pairs breeding in 4 nest-houses with a total of 54 compartments and was established in 1977. The houses could be lowered, and I caught males by placing traps in their nesting compartments. All birds were weighed with a 100 g Pesola scale, and their flattened wing chord was measured with a wing chord ruler.

Plumage manipulations. I conducted plumage manipulation experiments on territorial adult males between late March and early May, 1988 and 1990, which corresponds with the peak territory establishment period of males. I conducted paired experiments in which two males (a lightened and a control male) were manipulated on the same day, to compare more directly the effects of plumage color on intruder pressure. Most (10/12) paired experiments were done before mid-April, when adults had not begun nest building and most subadult males had not yet arrived. Males that defended similarly sized territories (number of cavities) not more than 15 m from each other were randomly assigned to the control or lightened group. There was no significant difference in body mass (Wilcoxon matched-pairs signed-ranks test; $T=22$, $n=9$, $P>0.10$) between control (mean = 54.0 g, SD = 3.3, $n=10$) and lightened (mean = 53.7 g, SD = 4.1, $n=12$) males. All males were mated prior to manipulations; since females also arrive very early in the spring, males are usually mated soon after territory establishment. Both males in a paired experiment were captured during the late morning or afternoon within 24 h of each other using nest traps. The male

was pinned on his back, with wings immobilized. For experimental birds, hair lightener (Naturally blonde, Clairol) was applied to the body feathers on the underside (chin, throat, breast, belly, and undertail coverts) for 12–15 min, leaving several small (0.5 cm²) patches on the breast and undertail coverts blue to mimic the splotchy appearance of subadult males. Feathers treated with hair lightener turned a pale yellow color. For control birds, shampoo was applied in the same way, and left for 12–15 min. The underside of the birds was then rinsed with warm water, shampooed, rinsed, then partially dried with paper towels. A hair dryer was used to dry feathers for three manipulations done in 1988, but this additional handling stressed the birds and so was not used subsequently. The entire procedure from time of capture typically took about 20–25 min. Care was taken to treat control birds in the same manner as experimental birds.

After release, I watched the male's nest site for 30–90 min to observe interactions with his mate and any intruders present on the territory when he returned. Several males were not resighted during this period but appeared later. I sampled intruder pressure over the next 2–3 mornings from 0600–1030, the peak period of intruder activity, by conducting 5–6 half-hour watches on each of the males. A total of 132 half-hour watches were performed on 12 control and 12 lightened males. During each watch, I noted the amount of time the male and female were on their territory, the number of "croak" songs (Brown 1984) given by the male, the number and behavior of male intruders on the territory, the duration of intrusions, and the response of the territory owners toward the intruders. The median value for each individual male was used for analysis.

Intruder-owner interactions were followed during two types of observation: focal owner and focal intruder watches (Stutchbury 1991b). Most intrusions were by individuals not known to be defending territories in the area (e.g., "floaters"), so only these were used in the analysis. In 1988, I observed intrusions on the territories of 20–25 males for 30 min periods during the morning, every 3–4 days. In 1989 and 1990, I carried out focal watches of intruders at UOBS in the morning by following the behavior of individual intruders as long as possible as they moved between territories (Stutchbury 1991c). For each intrusion I noted the plumage class and sex of the intruder (adult male, subadult male, or female), the duration of the intrusion, intruder behavior, and the aggressive response of the male and female owners.

Intruder behavior was categorized as perching on the edge of the nest-house roof over the territory, perching on the territory, perching with head inside the cavity (inspecting), and entering the cavity. An attack by the territory owner included displacements, chases, and actual fights. I did not include cases in which the territory owner was absent for the duration of the intrusion. Control subadults in other plumage manipulation experiments (Stutchbury 1991b) were included with unmanipulated subadults in analyses of intruder-owner interactions. Contingency tables were used to analyze owner aggression toward intruders. To reduce the problem of independence of intrusions and pseudoreplication (Hurlbert 1984), I used only one interaction between an individual intruder and individual territory owner per day, for each category of intruder behavior. I arbitrarily chose the first intrusion observed of that category per territory owner on the day in question. For analysis, I excluded intrusions occurring after early May, when most adult male pairs begin incubating and intrusions by adult male floaters become rare.

Results

Plumage-manipulation experiments

Lightened adult males did not suffer any increase in intruder pressure by males on their territory as a result of their loss of bright coloration (Table 1). The number

Table 1. The cost of territory defense (mean \pm SD) for control and lightened adult males ($n=12$ paired experiments). Measures of cost are the median number of male intruders/30 min, median duration of each intrusion, proportion of intruders to inspect or enter the cavity, median time the experimental male was on the territory per 30-min watch, and median number of songs/time on territory ($n=10$ for song rate). Statistics for Wilcoxon matched-pairs signed-ranks test (T); in all cases $P>0.10$

Costs of defense	Control	Lightened	T
Intrusions/30 min	2.38 \pm 2.38	1.83 \pm 1.57	25.5
Duration per intrusion (s)	44 \pm 47	32 \pm 19	31
Proportion of intruders to inspect or enter	0.12 \pm 0.12	0.11 \pm 0.14	19.5
Time on territory (min)	17.5 \pm 5.7	17.3 \pm 6.0	33
Male song rate (no./min)	0.76 \pm 0.27	0.52 \pm 0.40	17

of male intrusions per 30 min watch was not significantly different between treatment groups (Table 1). Intruder pressure is also a function of the duration of intrusions and extent of challenge to owners. However, there was no significant difference between control and lightened males in the duration of intrusions by males or the likelihood that intruders would challenge the owner by inspecting or entering a cavity (Table 1). Fights between owners and intruders were relatively uncommon; 4 of 12 control males and 2 of 12 lightened males were involved in one or two fights during all watches combined.

Control and lightened males also expended similar efforts on territorial defense (Table 1). There was no significant difference between lightened and control males in the time spent on their territory or the rate at which they sang while on their territory (Table 1).

During the time that males were removed from their territories, 2 of 11 control males and 7 of 12 lightened males had intruder males move onto the territory during their absence. The bias toward lightened males is unrelated to the plumage treatment, however, because the replacements arrived before the manipulated bird returned. In 5/7 cases lightened males were involved in fights to evict the intruders, whereas 0/2 control males fought with their replacements. Lightened males won these initial fights with adult male replacements in 3/5 cases; the other 2 lightened males were evicted from their territory. One of these evicted males was seen as a nonterritorial "floater" in the colony until obtaining a territory 14 days later.

Lightened males did not appear to have any difficulty in maintaining their territory compared with control males. The proportion of males that lost their territories was 1 of 15 for control males and 5 of 15 for lightened males (G -test; $G=3.26$, $df=1$, $0.10>P>0.05$). These proportions include 3 control and 3 lightened "floater" adult males that obtained territories after I had captured them in temporarily erected houses in late March 1989 and manipulated their plumage. Although there was a

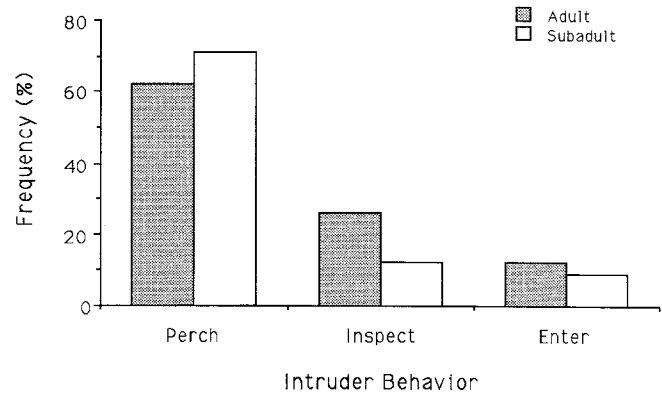


Fig. 1. Proportion of subadult male intruders that perched, inspected, and entered during intrusions on the territories of adult male ($n=335$ intrusions) and subadult male ($n=34$ intrusions) territory owners

Table 2. Aggressive response of subadult and adult male territory owners toward subadult male intruders early in the breeding season. Attacks include displacements, chases, and fights. Total number of intrusions given in parentheses

Intruder behavior	Proportion attacked (%)	
	Subadult owner	Adult owner
Perch on roof	0 (14)	1 (116)
Perch or inspect	29 (35)	21 (338)
Enter cavity	100 (3)	68 (44)

trend for lightened males to be more likely to lose their territories, I had no direct evidence that any of these males were evicted. In most cases, the males were replaced after they had disappeared for some other reason. All of these disappearances occurred in 1990, an unusually wet spring, which suggests that abandonment may have been related to poor food supplies.

Of the males that retained their territory, 1 of 9 lightened and 6 of 14 control males maintained the same territory size throughout the season (G -test, $G=2.88$, $df=1$, $0.01>P>0.05$). There was no significant difference (Mann-Whitney U -test, $U=29$, $N_1=8$, $N_2=8$, $P>0.10$) in the final territory size of males that did suffer some reduction in territory size (lightened: mean 2.3 cavities, SD 0.9; control: mean 2.1, SD 0.8).

Intruder-owner interactions

Intruding males that enter a nest cavity on the owner's territory run a high risk of being involved in a fight with the owner and almost always lose such fights (Stutchbury 1991 b, c). If intruder males are intimidated by owners with adult plumage, they should be less likely to escalate contests by attempting to enter cavities when intruding on adult male than subadult male territories. However, subadult male intruders were not less likely to enter nest cavities when intruding on adult male territories (Fig. 1); in fact, the trend was in the opposite direction (G -test, $G=4.8$, $df=2$, $0.10>P>0.05$).

The aggressive response of territory owners did not depend on their plumage color (Table 2). Adult and subadult male owners were equally likely to attack subadult male intruders early in the breeding season (G-tests, $df=1$, $P>0.10$). I could not compare territory owners in their response to adult male intruders, because few adult males are still floaters at the time subadults first acquire territories (Morton and Derrickson 1990; Stutchbury 1991b).

Discussion

Territory defense

I found no evidence that bright plumage in territory owners signals fighting ability or aggressive motivation towards intruders. Adult male purple martins whose bright plumage was manipulated to appear subadult-like did not suffer an increased intruder pressure or likelihood of losing their territory compared with control males (Table 1). There were also no significant differences between control and lightened males in indirect measures of the cost of territory defense (time spent on the territory, song rate, or frequency of fights with intruders). The bright plumage of control males did not deter intruders from visiting the territory or challenging the owner. These results are supported by data on the behavior of individual floaters. Subadult male floaters were as likely to escalate contests with adult male owners as subadult male owners (Fig. 1) and as likely to intrude on the territories of adult as subadult males (Stutchbury 1991c).

Rohwer and Roskaft (1989) suggested that the experimental removal of bright badges increases the costs of territorial defense only when the manipulation mimics a reliable signal of subordination. In other words, intruding males must assess dull plumage as a signal of owner vulnerability. Although subadult male martins are smaller and less experienced than adult males (Stutchbury 1991b), this does not necessarily reduce their ability to defend a territory. Adult and subadult males invested a similar effort in defending resources (Table 2). Owners usually win fights with intruders, regardless of plumage color (Stutchbury 1991c). Territory owners may differ little in their ability to defend territories because site dominance, as opposed to intrinsic fighting ability, determines the outcome of contests (Rohwer 1982).

Any differences in intrinsic fighting ability between owners and floaters are swamped by the large asymmetry in aggressive motivation resulting from site dominance. One would expect assessment of the owners and their plumage color signals by intruders to be important only after this asymmetry in site dominance has been reduced. The longer an owner is absent from his territory, the lower the asymmetry in site dominance between himself and a replacement male (Krebs 1982). There was a tendency for lightened males to be involved in more fights to reclaim their territories after their temporary removal compared with control males. This may indicate

that replacement males were less intimidated by lightened than control territory owners after the asymmetry in site dominance had been reduced.

Territory acquisition

If bright coloration does not play an important role in reducing the costs of territory defense, then why are older males bright? Territory defense is only one component of territoriality; individuals must first obtain a territory. Rohwer and Roskaft (1989) extended the arbitrary identity badge hypothesis to include intruders and suggested that conspicuous badges may be important in territory acquisition rather than territory defense. Nonterritorial males that are good fighters may benefit from being distinguishable from other intruders by the owner when they return to a given territory. This hypothesis assumes that territory owners will be more intimidated by challenges from good fighters and be less likely to escalate contests and risk injury against good fighters.

The results of plumage manipulation experiments in male purple martins provide evidence that adult coloration is important in territory acquisition. In 13/17 paired experiments, subadult males who were dyed to appear adult-like obtained a territory more quickly than the control subadults (Stutchbury 1991b). Further evidence comes from the opposite experiment (Stutchbury 1990). In 1989, two paired experiments were conducted in which nonterritorial adult males were captured in late March before they established permanent territories. In each case, one male was lightened with hair lightener to mimic the appearance of subadult males, while the other was sham-manipulated. In both experiments, the control bright male acquired a territory 10–14 days before the lightened male.

Bright plumage color in male floaters may facilitate territory acquisition because the badge signals a high aggressive motivation (Studd and Robertson 1985b) and intimidates territory owners. Although the emphasis of the badge theory has been on signaling fighting ability (Rohwer 1982; Rohwer and Roskaft 1989), reliable badges of status can also be maintained by signaling high aggressive motivation (Studd and Robertson 1985b). Fighting ability may be relatively easy to assess on the basis of cues other than plumage color, such as body size, weaponry, or resource ownership. However, an opponent's aggressive motivation, which stems from the value of the contested resource (Hammerstein 1981; Parker and Rubenstein 1981), is not easily assessed based on the same external cues. Badges of aggressive motivation should be important in contests in which the outcome is not determined by intrinsic fighting ability (Butcher and Rohwer 1989).

Nonterritorial martins acquire territories primarily by gaining control over one or more of the extra cavities defended by an owner and repeatedly intrude at a relatively small number of territories (Stutchbury 1991c). In this type of contest in which victory goes to the individual that persists longest (an "asymmetric war of attri-

tion”), contestants should attempt to assess asymmetries in intrinsic fighting ability and aggressive motivation (Hammerstein 1981; Parker and Rubenstein 1981). Although all territory owners have a huge initial advantage due to their site dominance, the cost to owners of defending a marginally valuable resource (surplus cavities) gives persistent intruders an advantage in territory acquisition (Stutchbury 1991c). Territory owners are expected to avoid prolonged contests and the accompanying costs of repeatedly repelling an intruder if they perceive the asymmetry to be against their favor (Parker and Rubenstein 1981).

In purple martins, owners likely gain little from assessing differences in intrinsic fighting ability among intruders, because intruders rarely win individual fights with owners (Stutchbury 1991c). However, assessing differences among intruders in aggressive motivation could be important because the higher the resource value to the intruder, the longer he is expected to persist in repeatedly intruding at the territory (Stutchbury 1991c). Adult male intruders have a higher motivation than subadults to persist in contests for nesting cavities because adults have some site dominance from previous breeding experience in the colony (Morton and Derrickson 1990), have higher expected reproductive success (Brown 1978) and success in extra-pair copulations (Morton et al. 1990), and greater certainty of paternity (Morton et al. 1990) than subadult males. Thus, by distinguishing themselves from the subadult age class, older males may be more intimidating to territory owners and acquire territories more easily.

The age-specific plumage and social role of 1-year-old males suggests that they are pursuing an alternate strategy, so “cheating” would not necessarily pay off. Although the subadult plumage does not improve a young male’s ability to compete with adult males, it may have an important role in competition among subadults (Morton and Derrickson 1990) or competition and survival in winter roosts (Stutchbury 1991b).

Differences among species

The role of bright badges in territory defense clearly varies among territorial passerines. Early plumage manipulation experiments on red-winged blackbirds found that bright badges did intimidate male intruders (Peek 1972; Smith 1972). In yellow warblers (*Dendroica petechia*), the amount of brown streaking in territorial males is correlated with the level of aggressive effort a male expends in defending resources (Studd and Robertson 1985b). However, in yellow-headed blackbirds (Rohwer and Roskaft 1989) and purple martins, bright plumage is not important in territory defense. In sharp contrast to studies on bright plumages in territorial systems, plumage variation in wintering flocks has been consistently shown to signal dominance status in different species (Rohwer 1975; Fugle et al. 1984; Holberton et al. 1987; Moller 1987). This may be a result of the relatively simple competitive situation in winter flocks: There is

Table 3. Predicted effectiveness of badges of intrinsic fighting ability and aggressive motivation in territory defense (intimidating intruders) and resource acquisition (intimidating owners), for different competitive situations (explanation in text)

Competitive situation	Badge for	
	Defense	Acquisition
Neighbor vs. owner	Yes	No
Floater vs. owner		
Wait on territory, replace	No	No
“Float” and replace	No	No
War of attrition insert	No	Yes
Evict owner	Yes	No

no territory ownership, the resources contested (food) are the same, and there are few alternative strategies for resource acquisition (but see Rohwer and Ewald 1981). In territorial systems, however, there is great diversity in the types of resources being contested and the behavioral strategies of territory intruders.

Nonterritorial “floater” males are generally assumed to wander widely in search of vulnerable owners to challenge and acquire territories by winning actual fights with owners (e.g., Rohwer and Roskaft 1989). However, for most species very little is known about the process of territory acquisition or floater tactics (Arcese 1989; Stutchbury 1991c). If floaters do obtain territories via eviction, they would benefit from assessing the competitive ability of owners (e.g., Arcese 1987, 1989) and presumably would avoid contests with owners signaling a high fighting ability (Rohwer 1982). However, signals of fighting ability or aggressive motivation by owners may not be effective if intruders are attempting to insert onto a territory, as in purple martins (Table 3).

In some species, floaters acquire territories primarily by filling vacancies from which owners have disappeared (Picman 1987; Stutchbury and Robertson 1987). In such species, the intruders are attempting to assess territory quality or occupancy status (Hansen and Rohwer 1986) and are not themselves an immediate threat to the owner. Owners would benefit little from intimidating such intruders, because no resources are being contested. Of course, owners may face the difficulty of distinguishing between intrusions by neighboring males (threatening) and floater males (nonthreatening). If owners are aggressive toward all intruders and fighting is risky, then floaters may indeed avoid owners that signal high aggression or fighting ability. However, the process that would select for bright badges in owners would be the intimidation of neighbors, rather than floaters (Table 3).

Tests of hypotheses for the origin and maintenance of badges will be confounded by the fact that owners and intruders often face more than one type of competitive situation. Even within a species, nonterritorial males may have a variety of strategies to acquire territories (Baeyens 1981; Jamieson and Zwickel 1983; Smith 1984; Eckman 1988). A comprehensive theory to explain the evolution of bright badges in territorial systems will have

to take into account this diversity in competitive situations and be integrated with other forms of signaling such as behavior and vocalizations.

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