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Territorial male color predicts agonistic behavior of conspecifics in a color polymorphic species

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Male cichlid fish, *Astatotilapia burtoni*, live in a lek-like social system in shore pools of Lake Tanganyika, Africa, as one of two distinct social phenotypes: territorial (T) males that comprise approximately 10–30% of the population and nonterritorial (NT) males that make up the rest. T males are brightly colored either blue or yellow with chromatic body patterns and are larger, reproductively capable, and defend territories containing a food resource used to entice females to spawn with them. NT males are camouflage colored, smaller, have regressed gonads, and shoal with females. Importantly, males shift between these social states depending on their success in aggressive encounters. It is not known whether there is a difference between yellow and blue T morphs. Here we asked whether T males preferentially defend their territory against a male of the same or opposite color. T males observed in social groups had agonistic interactions predominantly with neighboring T males of the opposite color, and yellow morphs initiated significantly more aggressive interactions. When agonistic preference was tested experimentally, T males had significantly more agonistic interactions toward males of the opposite color, and yellow T males became territorial in the majority of those interactions. Taken together, these results suggest that male coloration is an important social signal among neighboring T males in this species and support the hypothesis that T males differentially direct agonistic behavior depending on the color of neighboring males. *Key words:* aggression, polymorphism, social signal, territorial. *[Behav Ecol 18:318–323 (2007)]*

Color polymorphism among territorial (T) male phenotypes is relatively uncommon in most vertebrate species but often observed in fish and birds. In these species, color morphs typically correspond to particular behavioral profiles. For example, in pygmy swordtail fish (*Xiphophorus pygmaeus*), 13–25% of males are gold and the rest are blue (Baer et al. 1995). Although female swordtails prefer blue morphs, gold morphs dominate agonistic interactions (Kingston et al. 2003). Similarly, in midas cichlids (*Theraps citrinellum*), less than 10% of males are gold which are more aggressive and appear to have an advantage in agonistic interactions over gray morphs but no advantage among females (Barlow 1973; Barlow 1983b). This suggests that maintaining 2 morphs in a fish species may result from differential mate preference, agonistic interactions, and/or predation risk (Barlow 1983a; Kingston et al. 2003). In contrast, red and black morphs of male threespine sticklebacks, *Gasterosteus aculeatus*, do not show preferential agonistic behavior toward males of differing nuptial colors (McKinnon and McPhail 1996). Approximately 3.5% of bird species have color polymorphism, and for some species, these morphs have been shown to match distinctive behavioral patterns (Roulin 2004). For example, in white-throated sparrows (*Zonotrichia albicollis*), color morphs differ in agonistic and dominance and mate disassortatively (Knapton and Falls 1983; Watt et al. 1984).

Male–male competitive interactions for food, mates, and other resources are common throughout the animal kingdom. Aggressive competition is an important force in the formation and maintenance of dominance hierarchies that can be the defining characteristic of many social species (e.g., Wilson 1975), and male–male interactions have been hypothesized to contribute to the explosive speciation of cichlid fish species in the East African lakes (Seehausen and Schluter 2004). In *Astatotilapia burtoni*, from Lake Tanganyika, T males live in a lek-like social system, defending territories where they feed and spawn, whereas nonterritorial (NT) males mimic female behavior to gain access to food. These 2 phenotypes differ in coloration, behavior, and reproductive capacity (Fernald 1977; Fernald and Hirata 1977). To maintain territories, males interact aggressively using a range of behaviors from vigorous physical encounters to ritualized threats toward neighboring T males. T males also attack and chase NT males and females who always flee in the face of an attack. Males can rapidly switch phenotype, from territorial to nonterritorial and vice versa, depending on social circumstances. T males may have a background blue or yellow coloration, whereas NT males and females all express a brown/green camouflage pattern. Both blue and yellow body coloration lie well within the visual capacities of *A. burtoni* (Fernald and Liebman 1980).

Yellow and blue *A. burtoni* male morphs are approximately equally represented in the population, and these color differences have been hypothesized to be an adaptation to particular habitats (Robison 2000). Like other species that exhibit color polymorphism, T male *A. burtoni* on occasion exhibit a mixture of blue and yellow coloration although this is rare (personal observation). *Astatotilapia burtoni* males can change from yellow to blue and vice versa. A survey of 2423 adult males from a laboratory found 53% yellow NT, 9% blue NT, 20% yellow T, and 19% blue T males (Robison 2000). From this population, 64 males were selected of which 38 (59%) changed color during the 6-month observation (Robison 2000). Female *A. burtoni* do not appear to prefer one color morph over the other; however, they do prefer T males over NT males, and among T males, they prefer smaller more

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active males (Clement et al. 2005). Earlier work on other cichlid species suggested this genus may be selectively neutral with respect to mate choice among different color morphs (Seehausen and Van Alphen 1998).

The purpose of the experiments described here was to test whether T males of a given color differ in aggressive behavior directed toward conspecifics of the same or different color morphology. We hypothesized that T male color morphs are preferentially more aggressive toward males of the opposite color. We first observed animals in a seminatural environment. To test our hypothesis directly, we devised an agonistic preference procedure offering individuals an opportunity to indicate their preference between animals of the same or different color and measured their choices. Finally, we allowed direct interactions to discover the outcome of direct agonistic encounters.

METHODS

Animals

Astatotilapia burtoni derived from wild-caught populations were housed in aquaria under conditions mimicking their natural habitat: 29 °C, pH 8, and 12:12 h light:dark cycle with full spectrum illumination (Fernald 1977). A layer of gravel (~3 cm, thick) covered the bottom of the aquaria, and terracotta pots were placed in each tank as shelters to facilitate the establishment and maintenance of territories by males. Because T male *A. burtoni* infrequently exhibit a mixture of blue and yellow coloration, we chose males expressing discrete coloration of blue or yellow for 1 month to avoid any confound. Animals were fed ad libitum every morning with cichlid pellets and flakes (AquaDine, Healdsburg, CA). All animals were treated in accordance with the Stanford University Institutional Animal Care and Use Committee (IACUC) guidelines.

Observations in seminatural environment

Reproductively active adult *A. burtoni* were housed in groups of 7–9 females and 7–9 males in aquaria (85-cm length × 53.7-cm width × 30-cm depth). Animals were identified individually using randomized combinations of colored beads (excluding yellow and blue beads) attached just beneath the dorsal fin. Each aquaria used for observation had 2–4 yellow and 2–4 blue T males as well as NT males. A total of 43 animals were observed in 7 aquaria. The color distribution of T males was one aquarium with 4 blue and 2 yellow, another with 3 blue and 4 yellow, and another with 3 blue and 2 yellow; two aquaria with 2 blue and 2 yellow; and two with 2 blue and 3 yellow males. Each T male was observed for 10 min at 9 AM, 3 PM, and 9 PM over 4 consecutive days.

Aggressive behaviors directed toward other T males as well as toward NT males and females were identified and recorded using the following categories (Fernald 1977): 1) bite = bite an opponent; 2) side threat = sideward presentation of spread opercula, fins, and distended chin to an opponent; 3) border fight = confrontation between 2 T males at the site of their common border; 4) approach = swim quickly toward, then stop short near another fish, and 5) displaced aggression = biting, approaching, and chasing of females and NT males. Other behaviors recorded included spawning and shelter entries.

Test of agonistic preference

Colonies of animals in several aquaria were observed for 1 month, and T males ($N = 24$) that had maintained territories continuously for at least the previous 2 weeks were selected from 15 groups to achieve the number of animals to be tested as described below. As above, males were tagged with colored beads to allow identification. Test aquaria (85-cm length × 53.7-cm width × 30-cm depth) were divided into 3 equal compartments separated by a clear perforated barrier with one T male ($N = 3$ for each experiment) and one female in each compartment. The yellow or blue test male was placed in the middle compartment with a yellow "stimulus" male on one side and a blue "stimulus" male on the other side. The location of the stimulus males was counterbalanced. Females were present to stimulate reproductive and agonistic territorial behavior from the males in the experiment. NT males were not included to limit possible confounding behavioral interactions of neighboring T males with NT males. The T male (blue or yellow) in the middle section was allowed to interact with a yellow T male and a blue T male on either side for 4 days. This experiment was replicated 8 times (4 yellow and 4 blue test fish).

Agonistic behavior of the test male and his neighboring T opponents was recorded with a digital video camera (MiniDV, JVC) for 1 h beginning as animals were placed into the tank and for 30 min 3 h later. The second and third days, males were observed for 30 min twice a day at the same times as on the first day. For each behavioral recording session, the first 10 min after onset of behavioral interaction was scored. On the fourth day, as the lights came on, the dividers were removed and behavior and status (e.g., established territories) were recorded for 30 min. Slight modifications of the aggressive behaviors described above were used to score behavior in the preference tests because the animals could not physically contact each other. Bites were scored when both fish positioned themselves face to face against the divider with opened mouths and nipped at the divider. Approaches were scored when animals swam rapidly toward an opponent but stopped short of the clear divider.

Data analysis

Frequency of behavioral acts was compared between yellow and blue morphs by 2-tailed paired *t*-tests (Figures 1B,D and 2). Comparisons between yellow–yellow, blue–blue and blue–yellow frequencies of behavior were performed using 1-way analysis of variance (Figures 1A,C, 4, and 5). The level of significance was $P < 0.05$ using statistical software (SPSS 13.0 for Windows).

RESULTS

Observations in seminatural environment

In the seminatural environment, all T *A. burtoni* males frequently interacted agonistically with neighboring T males. Males exhibited differential agonistic tendencies depending on body color of their opponent relative to their own color. Yellow T males consistently initiated significantly more border displays [$F(3, 183) = 39.14$, $P < 0.0001$] (Figure 1A) and bites [$F(3, 174) = 5.99$, $P < 0.001$] (Figure 1B) toward blue T males when compared with males of the same color or blue males toward opposite and same colored males.

Whereas yellow T males exhibit more aggressive behavior toward blue T males, blue T males direct significantly ($t = -2.83$, $P < 0.008$) more aggressive acts toward the shoaling fish (females and NT males) when compared with yellow males (Figure 2A). There was no significant difference ($t = -1.13$, $P < 0.26$) for shelter/spawning site entries between yellow and blue T males (Figure 2B).

Agonistic preference test

As described for observations in seminatural conditions, male *A. burtoni* interacted agonistically with their neighboring

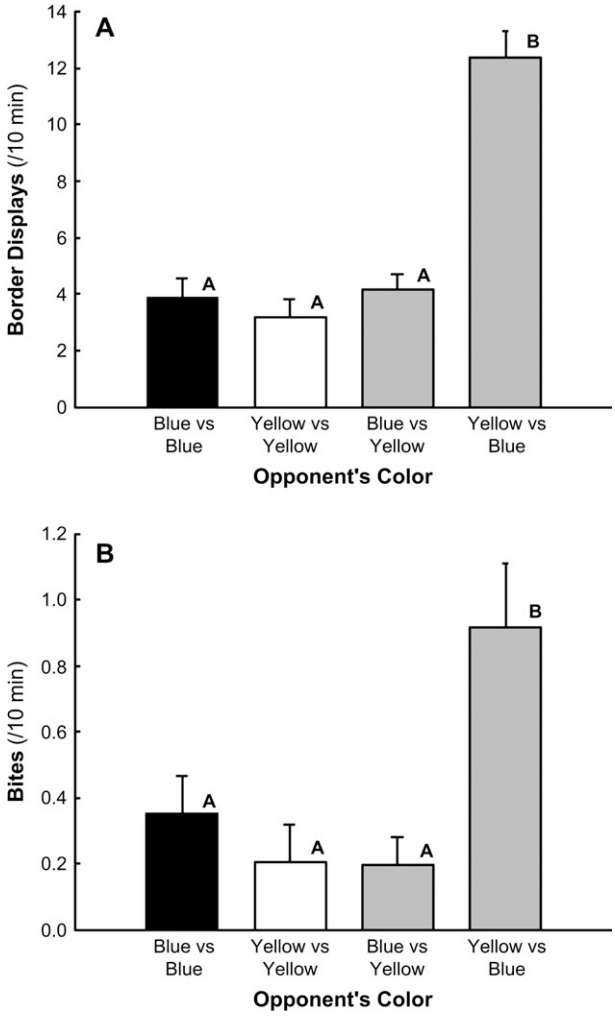

Figure 1
Ongoing border displays and bite rates observed between neighboring T males in a seminatural social system. The mean (±standard error of the mean) number of (A) border displays between T males plotted as a function of body color of the male initiating the display, which is labeled first for each pair and (B) bite rate during border encounters plotted as a function of body color and initiator as in (A) above. Mean values that share superscript symbols are not significantly different, and those with no common superscript symbols are significantly different ($P < 0.05$, see Methods).

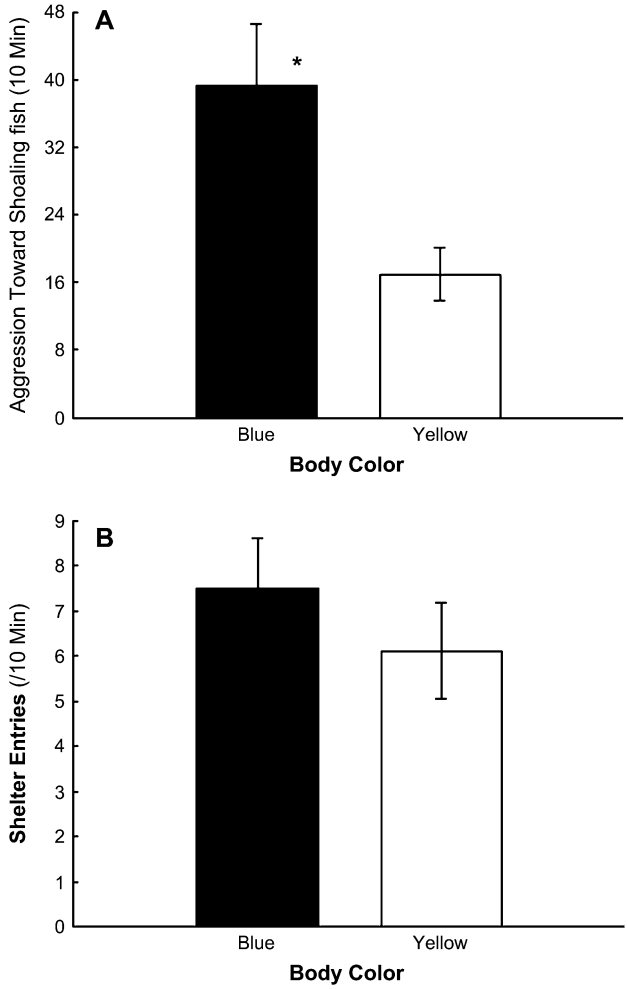

Figure 2
Agonistic acts toward shoaling fish (A) and shelter entries (B) observed between neighboring T males in a seminatural social system. The mean (±standard error of the mean) number of (A) aggressive acts toward shoaling fish or (B) shelter entries of T males with respect to body coloration. Means that share or do not have a superscript symbol are not significantly different, and those with no common superscript symbol are significantly different ($P < 0.05$).

T opponents and exhibited agonistic behavior differentially depending on the color of their opponents. When tested, T males spent significantly more time overall interacting with males of the opposite color (Figure 3B [$F(3, 24) = 11.27$, $P < 0.0001$]) and directed significantly more aggression toward males of the opposite color (Figure 3A [$F(3, 24) = 9.88$, $P < 0.0001$]) on the first day. Yellow T test males engage in significantly fewer aggressive bouts toward yellow opponents as compared with aggressive bouts between blue versus blue or blue versus yellow males (Figure 4A [$F(3, 92) = 25.59$, $P < 0.0001$]). Biting behavior directed toward an opponent through the clear Plexiglas dividers was significantly higher when test males interacted with a male of the opposite color when compared with males interacting with males of the same coloration (Figure 4B [$F(3, 96) = 3.89$, $P < 0.011$]).

For total level of aggression, there was an effect of opponent coloration ($P < 0.006$) and an effect of decreased aggression with time ($P < 0.001$). Interactions between blue versus yellow males resulted in significantly higher total aggression levels as compared with blue versus blue males interactions at 0 ($P = 0.003$) and 4 ($P < 0.01$) and yellow versus yellow males at 0 ($P < 0.019$) and 4 ($P < 0.013$) hours postintroduction. Whereas, interactions between yellow versus blue males resulted in significantly higher total aggression levels as compared with blue versus blue males interactions at 0 ($P = 0.0001$) and 4 ($P < 0.0001$) and yellow versus yellow males at 0 ($P < 0.0001$) and 4 ($P < 0.0001$) hours postintroduction (Figure 5A). For percentage of total aggression levels, there was an effect of opponent coloration ($P < 0.001$). Interactions between blue versus yellow males or yellow versus blue males resulted in significantly higher percentage of total aggression levels as compared with blue versus blue males ($P < 0.0007$ and $P < 0.001$, respectively) and yellow versus yellow males ($P < 0.001$ and $P < 0.002$) throughout the course of the experiment aquarium; however, there was no effect of time (Figure 5B).

When the barriers were removed, typically only one male was able to defend the entire territory successfully. Of the 8 tests, 5 times (71.4%) a yellow T male established a territory

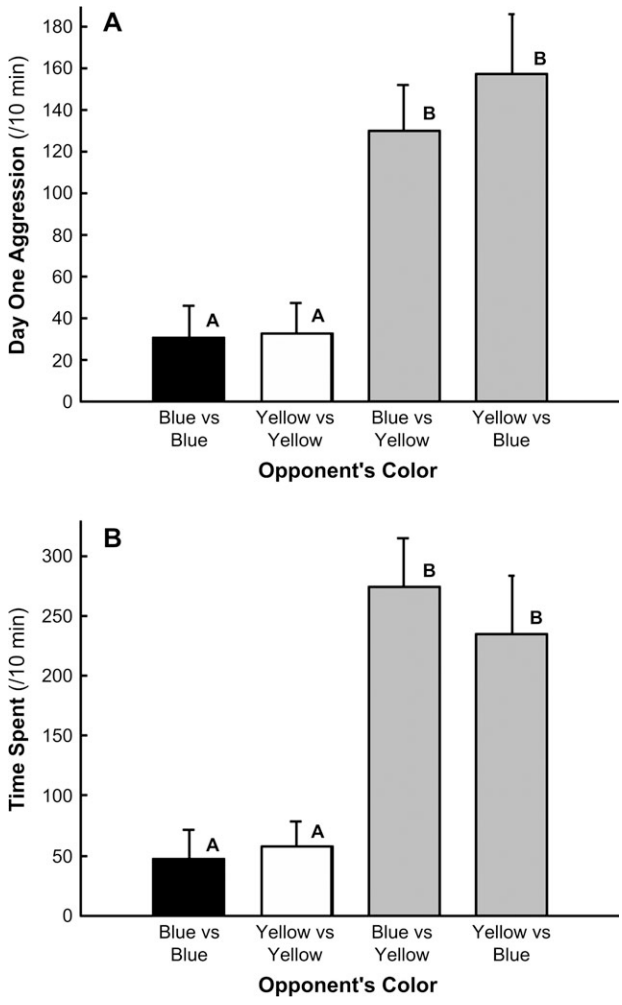

Figure 3
Aggressive acts (A) and time spent (B) adjacent to stimulus males as a function of male color in the preference test (see Methods). The mean (±standard error of the mean) amount of (A) aggressive acts on the first day or (B) time spent agonistically interacting by focal T male both plotted as a function of body color of the male initiating the display, which is labeled first for each pair. Interactions between males of opposite colors were significant in both measures ($P < 0.05$).

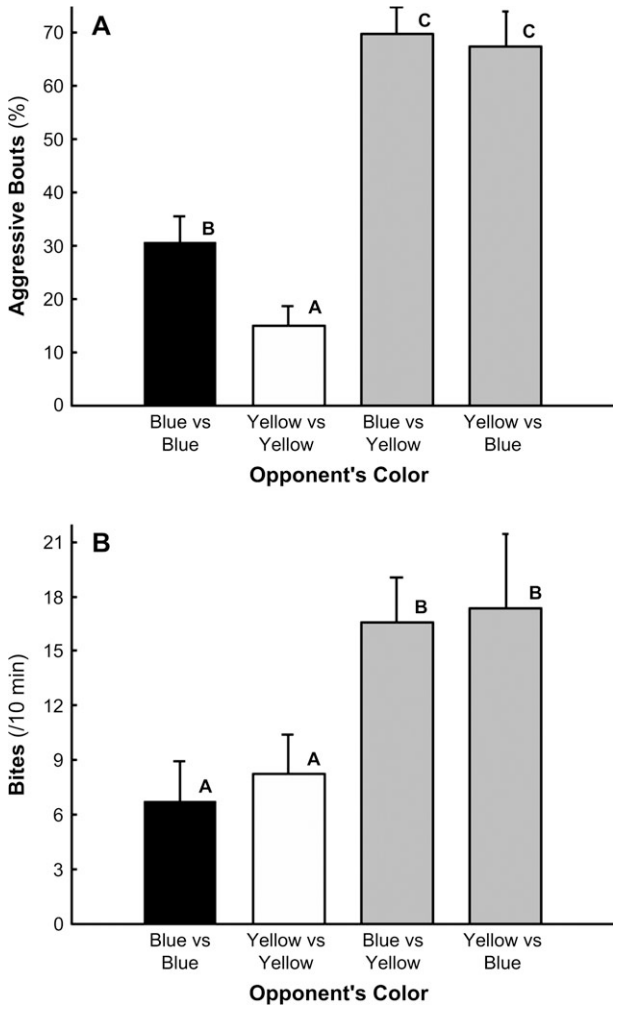

Figure 4
Aggressive bouts and biting behavior observed between neighboring T males during the preference test. The mean (±standard error of the mean) percentage of (A) aggressive bouts or (B) bites performed by focal T male plotted as a function of body color of the male initiating the display, which is labeled first for each pair. Means that share superscript symbols are not significantly different, and those with no common superscript symbols are significantly different ($P < 0.05$).

compared with 2 times (28.6%) for blue T males and once none of the 3 males established territories within the 30 min after barriers were removed (Figure 6).

DISCUSSION

Our data showed that yellow *A. burtoni* males preferentially act aggressively toward neighboring T males of the opposite color in a seminatural context and in agonistic preference tests both color morphs prefer to act agonistically with males of the opposite coloration. Over time, the frequency of aggressive acts between males decreases, but the same overall preference remains. Yellow morphs are more likely to act aggressively toward neighboring blue T males than yellow T males in seminatural conditions. Blue T males express higher levels of aggression toward the shoaling fish in the tank than do yellow T males. Taken together, these data suggest that coloration of the animals is a major explanatory factor in their aggressive behavior.

Suggestions about the possible selective advantages of animal colors have a long and illustrious history of observation and experimentation (Darwin 1859; Longley 1917; Roosevelt 1918). Early reports focused on colors in relation to concealment. For example, Longley conducted very simple experiments with reef fish placing food in various locations and documenting the color change of the fish as they swam from one background color to the next (Longley 1917). Roosevelt based his arguments about the role of coloration of animals on his hunting experience and observations of many different species in the wild. He posited that animals with cryptic coloration are only effective when the animal is perfectly still. Though each proposed different hypotheses about the role of color, Roosevelt and Longley agreed about the value of changing color to match the habitat.

More recently, color polymorphisms (e.g., coloration diversity within a species) have been related to correlated behavioral characteristics similar to those found for *A. burtoni* (cf. Kingston et al. 2003; Roulin 2004). In *A. burtoni* and other cichlids, many factors could contribute to the maintenance of color polymorphism such as habitat adaptation (Fernald and Hirata 1977), sexual selection (Barlow and Rogers 1978;

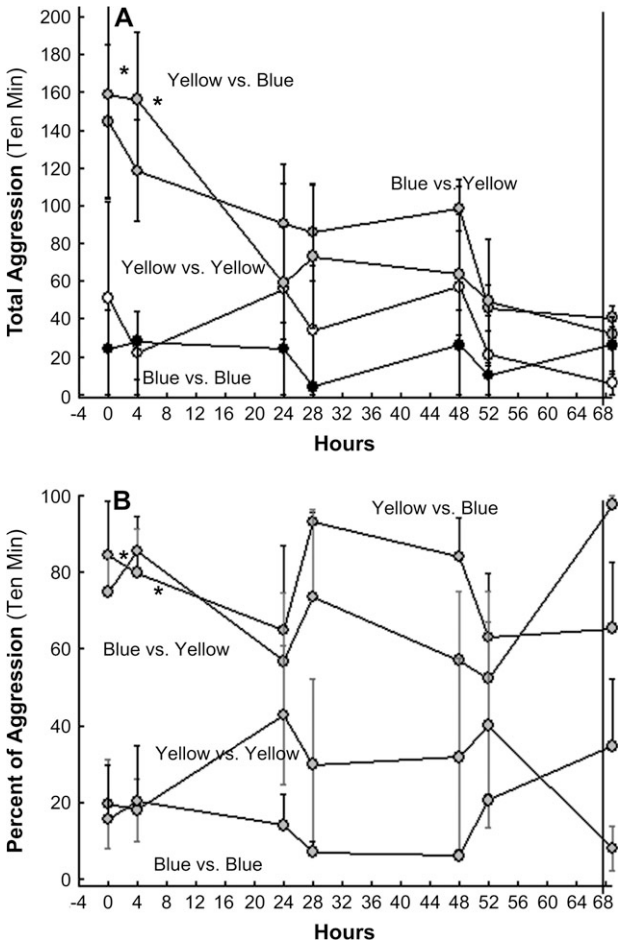

Figure 5
Total number of aggressive acts (A) and fraction of total aggressive acts (B) between neighboring T males plotted over the course of the preference test. Aggression toward T males of the opposite color morph was significantly elevated during the first day (A) and the fraction of aggressive acts expressed was elevated between males of opposite body color (B). At 68 h, the clear divider was removed (black vertical bar). Means that share superscript symbols are not significantly different, and those with no common superscript symbols are significantly different ($P < 0.05$).

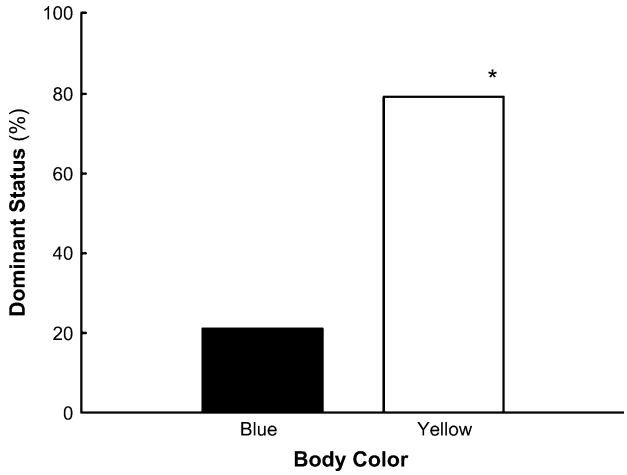

Figure 6
Percentage of yellow and blue color morphs acquiring territories following removal of clear barriers in the preference test (see text). Yellow T males acquire more territories than blue males.

Clement et al. 2005), and social interactions (Barlow 1983b; Seehausen and Schluter 2004). Collection of both yellow and blue morphs of *A. burtoni* males from the wild revealed that blue morphs were more common in shore pools and murky water, whereas yellow morphs were more common in open or clearer water. This suggests that each color morph may have an advantage depending on available habitat (Fernald and Hirata 1977). However, this original hypothesis that habitat may play a role in the yellow and blue morphs of *A. burtoni* appears not to be the central factor. Rather, these color morphs may instead depend on social interactions. In some species, sexual selection in the form of female mate preference influences the maintenance of polymorphism (Barlow and Rogers 1978; Kingston et al. 2003; Roulin 2004), although we know this is not the case in *A. burtoni* (Clement et al. 2005).

Polymorphic midas cichlid fish have a bias in agonistic behavior between similar color morphs as seen in *A. burtoni* (Barlow 1983b). More generally, male–male competition whether intra- or interspecies has been posited by Seehausen and Schluter (2004) to be a central force in the maintenance of polymorphism as well as the rapid speciation of cichlid fish in Lake Victoria in Africa. These authors suggest that closely related species of cichlids with similar coloration are less frequently found at spawning sites, but unrelated species of differing coloration are more frequently found. Specifically, they report that in males of 2 closely related species, *Pundamilia nyererei* (red nuptial colors) and *Pundamilia pundamilia* (blue nuptial colors), red males have an agonistic advantage and displace blue males. Blue males are distributed with greater geographic continuity, but red males, which are less frequent, always occur with blue males. Taken together, these studies suggest that differing agonistic tendencies of color polymorphic species may have contributed to the rapid speciation of cichlid fish in Lake Victoria. Based on previous work on agonistic behavior and hormone levels of teleosts, we suspect that the agonistic differences in the current study may be associated with circulating hormones.

In species with color polymorphism, different morphs are typically represented in varying frequencies in the population (Kingston et al. 2003; Roulin 2004). However, in *A. burtoni* yellow and blue morphs appear to be represented equally (Robison 2000). We postulate that the equal distribution of yellow and blue in *A. burtoni* T males might be maintained by the differences in agonistic behavior. In other species with similarly different color morphs (e.g., midas cichlids, swordtails *X. pygmaeus*, geckos *Gonatodes albogularis*), yellow coloration corresponds with the morph showing increased agonistic behavior and dominance during social interactions against other morphs in their species (Barlow 1983b; Ellingson et al. 1995; Kingston et al. 2003). Similarly, as shown here, yellow *A. burtoni* T males have increased agonistic behavior and dominance (Figures 1B, 2B, and 6). However, in midas cichlids and the other species noted, the frequency of yellow color morphs is low (~10–25%) in the population (Barlow 1983b; Ellingson et al. 1995; Kingston et al. 2003) in contrast to the approximately equal fraction found in *A. burtoni* populations. Previous work on the maintenance of color polymorphism in species has concentrated on a putative role in female mate preferences (Kingston et al. 2003; Roulin 2004). However, studies of the female preference of coloration for males in the genus *Haplochromis* and *Theraps* cichlids suggest female preference to be selectively neutral (Barlow and Rogers 1978; Seehausen and Van Alphen 1998).

Many species that exhibit color polymorphism also show differing agonistic tendencies, which in turn influence mating success (Kingston et al. 2003; Roulin 2004). Unlike the majority of polymorphic species expressing a color polymorphism,

A. burtoni males can change their color phenotype (Robison 2000). Two examples of polymorphic species that express similar flexibility in their phenotype are *Rana catesbeiana* and *Hyla regilla* (Camargo et al. 1999; Wente and Phillips 2003). In the frog *H. regilla*, approximately 22% of frogs are able to change body coloration (Wente and Phillips 2003). The color change is thought to be advantageous for matching foliage and changing seasons (Wente and Phillips 2003). Because color changes between morphs can occur, does agonistic behavior (in the case of *A. burtoni*) or habitat selection (in the case of *H. regilla*) change with body coloration? Future experiments should reveal whether the color change in *A. burtoni* males occurs in response to particular habitats or cohabitants. Alternatively, the color change may have a physiological basis in that specific color morphs are associated with particular combinations of internal parameters. This possibility can also be tested experimentally.

The data presented here suggest that body coloration of *A. burtoni* T males is an external signal of an agonistic response to other males. Whereas T males prefer to interact agonistically with neighboring T males of the opposite color in both experiments, the different behavioral strategies of more dominant yellow (more aggressive toward blue T males) and blue (more displaced aggression toward shoaling fish) T males in seminatural conditions could play a role in the maintenance of the observed color polymorphism through alternative behavioral strategies. Our data show that yellow T males are more aggressive toward blue T males in seminatural conditions. However, in the agonistic preference test, both yellow and blue T males exhibited more aggression toward T males of the opposite coloration. This difference may be a result in the different context of the interactions between the colony and the staged choices. In the seminatural situation, the yellow T males attack blue T males more than yellow T males but the blue T males do not. In this situation, it is possible that yellow T males may be simply more aggressive toward blue T males and blue T males express displaced aggression by attacking NT males and females. Whereas in agonistic preference test, the novel context of a new environment stimulates the animals' aggressive behavior toward males of the opposite color. This suggests that males of both morphs placed in a novel situation act aggressively toward the opposite color, but over time in a more natural context, the greater aggressivity in the yellow T males is expressed.

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