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Aggression and fighting ability are correlated in the swordtail fish *Xiphophorus cortezi*: the advantage of being barless

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Abstract Males of the swordtail fish *Xiphophorus cortezi* are polymorphic for the pigment pattern vertical bars. Previous studies indicate that barred males exhibit higher levels of aggression towards males with bars than those without, while barless males fail to exhibit differential levels of aggression to either morph. In this study I matched barred and barless males for size and paired them in dyadic contests in order to determine if either morph was more dominant and if so, if dominance was the result of higher aggression levels. I found that barless males had higher bite frequencies and were able to win a majority of the contests while barred males consistently escalated to biting first, even though in most cases they were ultimately the losers. In order to determine whether the observed aggression levels and fighting abilities were inherent to being barless or a consequence of responses to the bars themselves, the dyads were repaired once after barless males were given temporary bars and once after barred males had their bars removed. Thus, each morph encountered his opponent in both a barred and barless state. Regardless of bar state, naturally barless males continued to be more aggressive and more dominant than their barred counterparts. In addition, naturally barred males only won contests in which they bit more. These results indicate that for this species, aggression is an important component of winning contests when opponents are roughly the same size. As a result, naturally barless males as a whole appear to have higher resource holding potential (RHP) than naturally barred males of the same size because of their greater aggression levels.

Keywords Aggression · Color morphs · RHP · Vertical bars · *Xiphophorus*

Introduction

Aggression is thought to be an important component of fighting ability, and yet few studies have demonstrated that more aggressive males are more dominant (e.g. Ribowski and Franck 1993). One inherent problem in studying the relationship between aggression and fighting ability is that the expression of aggression is context specific. The relative size of one's opponent (e.g. Mayar and Berger 1992; Morris et al. 1995a), prior experience (e.g. Beaugrand et al. 1991; Beaugrand et al. 1996), and value of the contested resource (e.g. Dugatkin and Ohlsen 1990) are but a few of the factors known to influence how aggressive a male will be in a contest. Thus, in order to understand how aggression contributes to resource holding power (RHP) and contest outcome, asymmetries between opponents need to be either held constant or manipulated in such a way that they can be investigated independently of their effects.

Signals play an important role in many agonistic encounters and communication can affect whether an individual will behave aggressively or retreat. In general, the response to a threat signal is expected to be reduced aggression, as males can use this information to avoid the costs of a fight, and animals should refrain from engaging in contests in which they are the likely loser (Maynard 1973; Maynard 1976). Differences in male coloration are important in aggressive interactions in a range of taxa, including birds (Lemel and Wallin 1993; Pryke et al. 2002), lizards (Carpenter 1995; Baird et al. 1997), and fishes (Borowsky 1973; Martin 1977; Horth 2003) and may signal an individual's resource holding power (RHP), social rank, motivational state, or overall condition. In fishes, male coloration generally falls into one of two broad groups based on whether colors or color patterns can be quickly varied in response to context. In the first group are polychromatic species, whose males are "fixed" to a

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particular color morph. A classical example is that of the Midas Cichlid, *Theraps (Cichlasoma) citrinellum*, where both grey and gold morphs exist, the latter of which tend to be more aggressive and dominant (Barlow 1973; Barlow 1983a, b; Barlow, 1994). The second group consists of species whose males are able to rapidly change colors or color patterns. The ability to darken the body or parts of the body is commonly used as a signal in agonistic encounters and can signal either subordination (e.g., oscar cichlid *Astronotus ocellatus*, Beeching 1995; juvenile atlantic salmon *Salmo salar*, O'Connor et al. 1999) or dominance (e.g., juvenile guppies *Poecilia reticulata*, Martin and Hengstebeck 1981). Likewise, intensification of body coloration can be used to signal aggressive intent and conversely, suppression of coloration can be used to signal defeat or subordination (Moretz and Morris 2003).

The males of *Xiphophorus cortezi* are polymorphic for vertical bars, a pigment pattern found throughout swordtails (Rauchenberger et al. 1990). Much like *X. multilineatus* males (Morris et al. 1995b), barred *X. cortezi* males respond to the bars with reduced aggression (Moretz and Morris 2003). In *X. multilineatus*, however, only the smallest males lack bars, while in *X. cortezi* there is no correlation between size and having bars and the two morphs appear to occur with approximately the same frequency in nature (Morris et al. 2003). The bars on males that have this pigment pattern are usually visible when males are in their resting state. However, barred males have the ability to intensify the expression of the bars as well as suppress their expression, and use this signal during courtship with females and in contests with rival males. The bars have a heritable basis (Zimmerer and Kallman 1988) and like other male traits that serve dual functions, the evolution of the vertical bars may have been affected by both female choice and male–male competition. Females in this species have demonstrated a polymorphism in preference for the presence or absence of the bars (Morris et al. 2003), a preference for bar symmetry (Morris, 1998; Morris and Casey, 1998; Merry and Morris 2001), a preference for bar number (Morris 1998), and a preference for bar frequency (Morris et al. 2001). Likewise, *X. cortezi* males use the vertical bars in aggressive encounters much like other swordtail species; males intensify the expression of the bars at the onset of an aggressive encounter and bars fade in the subordinate male at contest's end (e.g., Zimmerer and Kallman 1988; Moretz and Morris 2003). In both staged contests and mirror image stimulation trials using males of this and several other swordtail species, intensification of the bars precedes aggressive behavior, and signals aggressive intent (Moretz and Morris 2003).

The purpose of this study was threefold. First, I wanted to determine whether one morph was more dominant than the other when matched for size in staged contests and if dominance was related to aggression levels. This is important in establishing whether there is a link between dominance and aggression. Such a link, if correlated with being either naturally barred or barless, would indicate that size for size, one morph would have higher RHP than the other. Second, I wanted to determine whether contest dynamics were af-

ected by the presence or absence of bars. Manipulating the presence of the bars on both morphs allowed me to establish whether initiation and escalation decision rules were affected by the presence or absence of bars, or whether the decision rules were correlated with a particular morph and not context dependent. Finally, I was interested in determining whether relative aggression levels were context dependent or an inherent property of being naturally barred or barless. By manipulating the bars and presenting each male with his opponent in a different context, it was possible to determine whether contest outcome and aggression levels are the result of aggressive responses to the bars or whether one morph has an advantage that is independent of bar state.

The impetus for these questions came from two previous studies. In the first, Moretz (2003) used a novel contest pairing procedure to obtain an approximation of RHP for males relative to other males in a tournament. Revaluation of these data indicate that of the males that were ranked higher than would be expected if size alone explained RHP, most were barless. Additionally, while contest dynamics in the previous study were reported in terms of smaller males versus larger males and winners versus losers, there was not a comparison of contest dynamics of barred males versus barless males. The current study allows for this comparison while controlling for the confounding effects of relative size. In the second study, Moretz and Morris (2003) found that only naturally barred males responded to the bars, and they did so with decreased aggression towards their barred mirror image. Even though barred males were more aggressive towards their barless mirror images than their barred mirror images, naturally barless males exhibited higher levels of aggression than did barred males in either state.

Methods

Study species

Xiphophorus cortezi are small live-bearing fish that inhabit pools of streams and rivers in northeastern Mexico. The *X. cortezi* males used in this study were collected from the Rio Axtla in San Luis Potosi, Mexico over a period of 3 years (June 1999, March 2000, and December 2001). At the end of each collection trip males were brought back to the laboratory at Ohio University where they were individually housed in 20 l tanks and visually isolated from one another. Fish were fed daily and maintained on a 14 h light/10 h dark photoperiod at a constant room temperature of 22°C. Two weeks prior to the beginning of the contests, males were anesthetized with tricaine methanesulphonate (MS-222) in order to accurately weigh and measure each individual (SL, standard length).

Experimental design

Sixteen pairs of males (1 barred, 1 barless male) were matched for size (SL). The size difference between the opponents ranged from 0.1 to 0.7 mm ($\bar{x} = 0.38$, SD

= 0.17). Each pair was placed in a 150 l aquarium and separated by an opaque plexi-glass divider for 24 h. The contest began by removing the divider and allowing the two males to interact. Data were recorded by direct observation and included which male initiated the contest (first display), which male escalated (first bite), and which male won. The total number of bites for each male was also recorded and bite frequency was calculated as bites/min (bpm). A male was determined to be the loser when he retreated from his opponent with his dorsal fins lowered and continued to retreat whenever approached. There were no instances of a male signaling defeat and then attacking. Males were visually inspected after each contest and none appeared injured. Likewise, there was no indication that males were overly stressed, as they appeared to behave normally (e.g., they continued feeding) after returning to their individual tanks.

There were three phases to the contests. The first phase consisted of contests between pairs in their natural bar state (naturally barless vs. naturally barred). After this first phase, I performed a series of manipulations. The second phase took place 3 weeks later, which was long enough to control for winner and loser effects, as well as opponent recognition from the previous encounter (Moretz 2003). The same males were re-paired after temporary bars were applied to the naturally barless males using antiseptic dye (Hoefer and Morris 1999). To control for possible handling effects, the naturally barred males were pseudo-painted using water instead of the dye. The number of bars painted on each barless male matched the number of bars on his naturally barred opponent (min = 4, max = 8). The contests were performed 30 min after the manipulations and the same data were collected as described above. In the third phase, I removed the bars of naturally barred males by freeze branding the pigmented area with dry ice (Raleigh et al. 1973) after anesthetizing the fish with MS-222. To control for possible effects associated with branding the fish, naturally barless males were also freeze branded. Three weeks later, the males were then re-paired with the same males for the final round of contests and the same data were recorded as described above. In addition to the above controls, previous studies have demonstrated that neither technique harms the fish or otherwise alters their behaviors (Morris et al. 1995b; Hoefer and Morris 1999; Moretz and Morris 2003). Likewise, visual inspections of the fish did not reveal any obvious injuries or changes in behaviors.

Statistical analyses

All analyses were performed using the statistical package NCSS (Hintze 2001). In determining whether barred or barless males were more likely to initiate the contests, escalate first in the contests, or win more contests, logistic regressions were used where the trials were the experimental units (Carpenter 1995; Zucker and Murray 1996). Likewise, logistic regressions were used to analyze the same aspects of contest dynamics as above but in terms of contest winners and losers. I used repeated measures ANOVAs to determine if either barred or barless males had higher bite frequencies and if either contest winners or losers had higher bite frequencies. Repeated measures ANOVAs were also used to determine if contest bite frequencies varied across the three experimental phases.

Results

Bouts typically began when one male approached his opponent and displayed either vertically in a headstand orientation or laterally. If the male was naturally barred, his bars either intensified prior to his displaying or during his displays (i.e., before escalating to biting) and this was true whether he faced a barless opponent or one that had been given temporary bars. Opponents usually responded by displaying and this continued until one male escalated by biting. All contests escalated to biting. Both males continued to display and bite throughout the encounter until one male signaled defeat by lowering his dorsal fin and swimming away. If the losing male was naturally barred, his bars also faded during this time. There were no observable differences between naturally barred and barless males in terms of the types of behaviors or displays used in any of the contests.

Phase 1—both males in their natural bar state

Barless males won 12 of the 16 contests against barred males (Table 1). Neither barred nor barless males were more likely to initiate the encounter (logistic regression: $\chi^2 = 0.29$, $df = 1$, $p = 0.59$, 56.3% correct model classification), however barred males were more likely to escalate first (Table 1). Contest winners bit more in more contests than did losers ($\chi^2 = 12.77$, $df = 1$, $p = 0.0005$,

Table 1 Number of first escalations and contests won by natural bar morphs for each of the three experimental phases^a

Phase	Escalation		χ^2	p	Model%	Contests won				
	Barred	Barless				Barred	Barless	χ^2	p	Model %
1	13	3	6.90	0.009	81.3	4	12	4.19	0.04	75.0
2	7	9	0.29	0.59	56.3	2	14	12.17	0.001	87.5
3	12	4	4.56	0.03	75.0	3	13	6.90	0.009	81.3

^aAnalyses were performed using logistic regressions with $df = 1$. Model% indicates the percent of individuals correctly classified by the logistic regression model. In phase 1, both males are in their natural bar state. In phase 2, temporary bars have been applied to the naturally barless males. In phase 3, the bars have been removed from the naturally barred males.

87.5%), though winners were neither more likely to initiate ($\chi^2 = 2.76$, $df = 1$, $p = 0.097$, 68.8%) nor escalate ($\chi^2 = 2.35$, $df = 1$, $p = 0.126$, 68.8%) than were contest losers.

Phase 2—artificial bars applied to naturally barless males, barred males in their natural state

Naturally barless continued to win more contests when given artificial bars, winning two more contests (14 of 16) against naturally barred males in phase 2 than in phase 1 (Table 1). Of the four barred contest winners in phase 1, only one was successful in phase 2. There was one barred male that won for the first time in phase 2. As in phase 1, neither barred nor barless males were more likely to initiate the encounter ($\chi^2 = 0.25$, $df = 1$, $p = 0.61$, 56.3%). However, unlike in phase 1 where barred males were more likely to escalate first, neither morph was more likely to escalate first in phase 2 (Table 1). Like phase 1, winners were neither more likely to initiate ($\chi^2 = 3.06$, $df = 1$, $p = 0.08$, 68.8%) nor escalate ($\chi^2 = 0.02$, $df = 1$, $p = 0.89$, 62.5%) than were contest losers. Contest winners bit more in a greater proportion of contests than did losers ($\chi^2 = 9.71$, $df = 1$, $p = 0.002$, 81.3%).

Phase 3—bars removed from naturally barred males, barless males in their natural state

Naturally barless males won 13 of the 16 contests against barred males with their bars removed (Table 1). Of the three naturally barred contest winners, only one won in both the previous two phases, while one was a previous winner in phase 1. The remaining naturally barred winner won for the first time in phase 3. As in the two previous phases, neither barred nor barless males were more likely to initiate the encounter ($\chi^2 = 0.01$, $df = 1$, $p > 0.99$, 50%). However, as in phase 1 but not phase 2, the naturally barred males were more likely to escalate first (Table 1). Winners bit more in more contests than did losers ($\chi^2 = 6.90$, $df = 1$, $p = 0.009$, 81.3%), though contest winners were neither more likely to initiate ($\chi^2 = 0.25$, $df = 1$, $p = 0.61$, 56.3%) nor escalate first in more contests ($\chi^2 = 0.91$, $df = 1$, $p = 0.34$, 62.5%) than contest losers.

Across phase analysis

Contest intensity as a whole, measured by the mean bite frequency of each pair, did not vary across phases (phase 1: $\bar{x} = 10.4$ bpm, SE = 1.16; phase 2: $\bar{x} = 8.7$ bpm, SE = 0.65; phase 3: $\bar{x} = 11.6$ bpm, SE = 0.98; $F_{2,47} = 2.76$, $p = 0.08$). Naturally barless males had higher bite frequencies than naturally barred males regardless of treatment (Fig. 1; $F_{1,95} = 15.61$, $p < 0.0004$; morph by phase interaction $F_{2,95} = 0.31$, $p = 0.74$) and frequency of bites was not affected by treatment for either morph (Fig. 1; barless, $F_{2,47} = 3.04$,

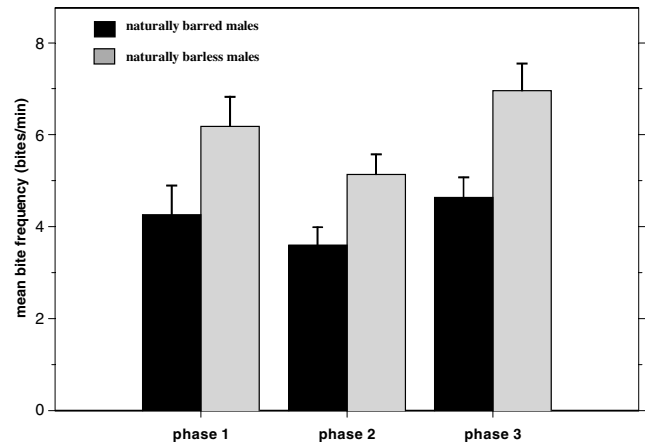


Fig. 1 Mean bite frequency for naturally barred and naturally barless *X. cortezi* males in matched size contests across three experimental conditions (phases). In phase 1, both males are in their natural bar state. In phase 2, temporary bars have been applied to the naturally barless males. In phase 3, the bars have been removed from the naturally barred males. Error bars indicate standard error

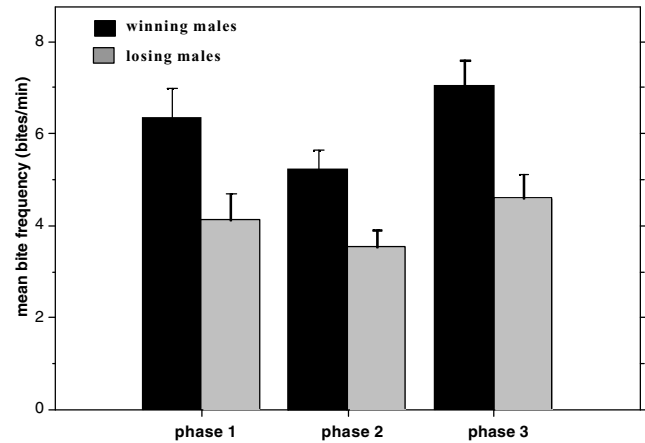


Fig. 2 Mean bite frequency for contest winners and losers of sized matched *X. cortezi* males across three experimental conditions (phases). In phase 1, both males are in their natural bar state. In phase 2, temporary bars have been applied to the naturally barless males. In phase 3, the bars have been removed from the naturally barred males. Error bars indicate standard error

$p = 0.06$; barred, $F_{2,47} = 1.23$, $p = 0.31$). Contest winners had higher bite frequencies than contest losers regardless of phase (Fig. 2; $F_{1,95} = 20.67$, $p < 0.0001$; outcome by phase interaction $F_{2,95} = 0.30$, $p = 0.73$). For all three phases, barred males only won contests in which they had the higher bite frequency. There was a significant difference in mean bite frequency difference between two opponents when naturally barred males won ($\bar{x} = 0.49$ bpm difference, SE = 0.009) versus when naturally barless males won ($\bar{x} = 2.84$ bpm difference, SE = 0.27; $t_{44.9} = 8.19$, $p < 0.00001$) which suggest that even small differences in aggression may be important in deciding contest outcome and lends further support for higher aggression levels in naturally barless males.

Discussion

Naturally barless males had a clear advantage over naturally barred males and were able to win a majority of the contests regardless of whether the signal vertical bars had been experimentally added or removed. As the bar manipulations did not affect contest outcome (naturally barless males won a significant proportion of contests in all three phases), it would appear that the superior fighting abilities of naturally barless males are an inherent property of being barless, and not the result of responses to the bars themselves. Size for size, naturally barless males as a whole appear to have higher RHP than naturally barred males and the fighting advantage enjoyed by naturally barless males seems to be related in part to their higher aggressive state. Much like the results reported by Moretz and Morris (2003) where males were presented with both their barred and barless mirror images, in this study, naturally barless males had higher bite frequencies than naturally barred males regardless of treatment. Likewise, in this study barred males only won contests in which they were more aggressive, though occasionally losing encounters in which they bit more than their opponent. As contests are usually decided by asymmetries in RHP (Parker 1974; Maynard and Parker 1976; Hammerstein 1981; Archer 1988), the deciding factor in these trials, where the confounding aspect of relative size has been removed, seems to be differences in aggression levels. However, aggression and contest outcome or dominance are not always correlated (e.g., Fitzgerald and Kedney 1987) and typically, an organism's size relative to that of its opponent is an important factor in winning or losing a fight (Archer 1988). In *X. cortezi*, when opponents are not matched for size, contest outcome is largely decided by size asymmetries (Moretz 2003). In addition, there is no correlation between winning or losing a fight and aggression levels, or being larger or smaller than an opponent and aggression levels (Moretz 2003). Thus, in this species, body size is the most important factor in the ability of males to obtain and defend territories, while relative aggression levels are an important factor when the size difference between two individuals is negligible.

An obvious question would be why selection would favor increased or decreased aggression in one morph and not the other. There are at least two, non-mutually exclusive hypotheses to account for the differences in aggression levels between the two natural bar types. The first focuses on selection for reduced aggression in barred males. As there is a correlation between having the genotype for the bars and having a response to the bars (Moretz and Morris 2003), and barred males in this species respond to the bars with decreased aggression, it is possible that their overall levels of aggression have been affected as well. In other words, their maximum aggression levels, which are exhibited when encountering barless males, may be limited as a result of decreased aggression toward barred males. This scenario necessarily assumes that there is a tradeoff between decreased aggression towards barred males on the one hand and increased aggression towards barless opponents on the

other hand. Thus, selection for decreased aggression in response to the bars may have reduced their overall aggression levels, requiring that the benefits resulting from decreased aggression towards barred males override any costs that result from being less aggressive than barless males. However, it is also possible that lower overall aggression levels in barred males may not be the result of a tradeoff but rather selection for lower overall aggression levels as well. This implies that the benefits of decreased aggression in response to the bars are also gained as a result of lower overall aggression levels. The second hypothesis focuses on selection due to the aggressive responses of other males. Barless males may be more aggressive because regardless of their opponent, there is no inhibition of aggression. Barless males either face other barless males that have high aggression levels or barred males who behave more aggressively towards barless males than barred males. As such, selection may have favored increased aggression in this morph as compared to barred males. Likewise, if there is a tradeoff for barred males between reduced aggression in response to the bars and maximum aggression levels, barless males would not be subject to this tradeoff, as barred males do not exhibit decreased aggression to the bars.

Neither naturally barred nor naturally barless males were more likely to initiate the contests (regardless of treatment), though naturally barless males had overall higher bite frequencies. However, naturally barred males were more likely to escalate first against barless opponents (phase 1 and in phase 3). In phase 2, where both males possessed bars, neither of the two morphs was more likely to escalate first. These results bring to attention two important points. The first is that there is a clear decision rule for the naturally barred males to escalate sooner whenever encountering a barless male, which resulted in barred males escalating before barless males in phases 1 and 3. This response seems to be both inherent to being naturally barred, as only the barred males demonstrated a tendency to escalate first, and context dependent as naturally barred males changed their escalation strategy based on the presence or absence of bars on their opponent. The second point seems counterintuitive: the less aggressive (in terms of bite frequencies) of the two morphs is in essence behaving more aggressively by biting first. The status-signaling hypothesis predicts quite the opposite (Rohwer 1975). Fundamentally, this hypothesis proposes that coloration can accurately convey information about rank or dominance and that this information can be used by subordinate individuals to avoid potentially costly interactions (Rohwer 1982; Senar and Camerino 1998), thus naturally barred males should avoid contests with barless males. Naturally barless males on the other hand, might be predicted to escalate first if males with greater fighting ability have less to gain by avoiding confrontations (Hurd 1997; but see Maan et al. 2001). However, in some instances it is the likely loser of contests that are expected to escalate first. In the Just and Morris (2003) model, an evolutionary stable strategy (ESS) is possible where males with lesser RHP initiate escalation, and the aggressive behaviors of likely losers are a direct

consequence of moderate differences in RHP. In this model, if likely winners can count on likely losers to either escalate or retreat, then it may pay the probable winner to leave the initiative to the likely loser in the hope that he may retreat (possibly by mistake), in which case a costly fight would be avoided. Alternatively, as contests with these fish do not result in injury and naturally barred males are able to win occasionally, it may pay probable losers to ignore the apparent fighting asymmetries and test their opponents (Grafen 1987).

In the swordtail *X. pygmaeus*, both male aggressive behavior and female mating preferences appear important in maintaining the blue/gold polymorphism found in males (Kingston et al. 2003). Gold males are more successful in agonistic encounters than are blue males, and gold males actively pursue females to a greater extent than do blue males (possibly resulting in more forced copulations). The advantage of gold males appears to be offset by female preference for blue males, though other factors such as predation and selection on traits correlated with color morph may also play a role in the maintenance of this polymorphism (Kingston et al. 2003). The maintenance of the polymorphism in *X. cortezi* is less clear. In the absence of female mating preferences, a correlation between male competitive advantage and reproductive success would favor barless males, due to their higher levels of aggression and dominance. However, females are polymorphic in their preference, with some females having a preference for barred males and others having a preference for barless males (Morris et al. 2003). While female preference likely plays a role in the maintenance of the bar polymorphism, it probably does not offset the competitive advantage of barless males to the extent that female preference in *X. pygmaeus* offsets the competitive advantage of gold males. As a result, it seems likely that other factors also play a role in the maintenance of the bar polymorphism in *X. cortezi*. For example, increased aggression may have additional costs, such as increased mortality as a result of higher hormone levels (e.g., reduced immune system response, Alfredo et al. 1996), an increased risk of injury, or increased predation (e.g., Jakobsson et al. 1995) resulting from higher levels of conspicuous behaviors (increased number of contests). Thus, the benefits associated with dominance may be offset by potential costs, leaving neither morph with a clear advantage due to male–male competition. However, relative predation and injury rates in the field between the two morphs are not known, and further studies are needed in order to fully understand the maintenance of this polymorphism.

In summary, I matched barred and barless males for size and paired them in dyadic contests. I found that naturally barless males had higher bite frequencies and were able to win a majority of the contests while barred males consistently escalated to biting first, even though in most cases they were ultimately the losers. In cases where barred males were able to win the contests, they had higher aggression levels than their barless opponents. Taken together, these results indicate that in this species, aggression is an important factor of contest outcome when opponents are evenly

matched for size. Regardless of bar treatment, naturally barless males continued to be more aggressive and more dominant than their barred counterparts suggesting that higher aggression levels and dominance appear to be an inherent property of being barless rather than context resulting from responses to the bars themselves. As a result, naturally barless males as a whole appear to have higher RHP than naturally barred males of the same size because of their greater aggression levels. While relative size is a determining factor of contest outcome in many systems, and as such often correlated with RHP, aggression levels may also be an important component of an individual's RHP.

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