



Motivation but not body size influences territorial contest dynamics in a wild cichlid fish



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Contests over resources are a key facet of social behaviour and have received extensive theoretical attention. However, the assumptions and predictions of the theoretical models have rarely been tested experimentally in wild free-living vertebrates. Here, we look at resource contests in wild *Neolamprologus pulcher*, a cooperatively breeding cichlid fish that lives in permanent territories in Lake Tanganyika, Africa. To elicit a contest, we removed a dominant breeding male from his territory and held him for either a short (4.5 h) or a long (20 h) period. The original resident male was then returned to his territory, which typically resulted in an aggressive contest with a usurping male that had taken over in the original resident's absence. We found that contests were shorter than those previously observed in a laboratory setting, with more physically aggressive attacks. Contrary to our predictions, the relative size difference between the males had no effect on contest dynamics or outcome, probably because all of the males involved in these contests were similar in body size. Instead, motivational factors influenced contest dynamics. Longer original resident removal times increased usurper male aggression, as well as the duration and intensity of the contests. Original residents were more aggressive when contesting over their sole territory (socially monogamous) than when contesting over one of their multiple territories (socially polygynous). Usurpers won more contests overall, and more aggressive fish were more likely to win contests. To our knowledge, this is the first study to examine resource contests in wild free-swimming cichlids, and our results reveal that subjective resource value is a primary driver of the dynamics and outcome of territorial conflicts among dominant *N. pulcher* males. Our results further suggest that respect for ownership may reduce conflict in *N. pulcher* and be important in governing colony structure.

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Across the animal kingdom, individuals compete over limited resources such as food or mating opportunities. These conflicts are often resolved through direct aggressive interactions (Briffa & Sneddon, 2010). Escalated fights can be costly in terms of risk of injury, energy expenditure, exposure to predators and time dedicated to fighting that could be spent engaging in other activities (Briffa & Elwood, 2004; DeCarvalho, Watson, & Field, 2004; Kelly & Godin, 2001). Therefore, most animals use ritualized displays and

assessment strategies to attenuate the costs of fighting and avoid escalated contests when possible (Arnott & Elwood, 2009; Clutton-Brock et al., 1979; Elwood & Arnott, 2012; Huntingford, Turner, & Downie, 1987; Parker, 1974; Parker & Rubenstein, 1981; Parker & Stuart, 1976; Smith & Parker, 1976). The importance of contests for securing critical resources, combined with the costliness of escalated contests, means that understanding the dynamics of resource contests provides a valuable window into the decision-making process in animals (Arnott & Elwood, 2008, 2009; Elwood & Arnott, 2012).

Theoretical models predict that the dynamics and outcome of resource contests will be influenced by a variety of factors, including the resource-holding potential of the individuals involved in the contest, the objective value of the contested resources and the subjective resource value or motivation of the

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contesting individuals. Resource-holding potential (RHP) is the physical ability for each individual to win an unrestrained fight (Arnott & Elwood, 2009; Parker, 1974; Parker & Stuart, 1976; Stuart-Fox, 2006). RHP is influenced by a variety of factors (reviewed in Arnott & Elwood, 2009), including body size (Clutton-Brock et al., 1979; Englund & Olsson, 1990; Enquist, Leimar, Ljungberg, Mallner, & Segerdahl, 1990), weaponry (Kelly, 2006; Sneddon, Huntingford, & Taylor, 1997) and physiological state (Stutt & Wilmer, 1998). All other factors being equal, the contestant with the higher RHP in a contest is more likely to win, since individuals with higher RHP are capable of incurring and inflicting higher costs during contests than individuals with lower RHP (Arnott & Elwood, 2009). In general, individuals are also expected to bear higher costs in order to obtain a more valuable resource (reviewed in Arnott & Elwood, 2008). For example, game theory models predict that individuals will incur costs up to a threshold equal to the value of the contested resource (e.g. 'war of attrition' models; Bishop et al., 1978; Hammerstein & Parker, 1982). Finally, subjective resource value (or motivation; Enquist, 1985; Barlow et al., 1986), can differ for each participant involved in the contest (reviewed in Arnott & Elwood, 2008). For example, food-deprived individuals might fight more vigorously for access to food resources than well-fed individuals (Hansen, 1986; Popp, 1987), and individuals in better reproductive condition might fight harder for access to mates than individuals that are less capable of reproducing (Neat, Huntingford, & Beveridge, 1998).

Prior residency is another factor that can have a strong influence on contest outcome (Wilson, 1975). Territorial residents consistently show an advantage over intruders in territorial conflicts (Alcock, 2013; Kemp & Wiklund, 2004; Kokko, López-Sepulcre, & Morrell, 2006; Olsson & Shine, 2000). This may occur for a variety of reasons, including greater value placed on the resource by its current owner (i.e. differences in subjective resource value; Johnsson & Forser, 2002; Krebs, 1982). Residents may also be more likely to win contests for physiological reasons, because there are self-reinforcing effects of prior winning experience (Earley et al., 2013; Goubault & Decuignière, 2012; Hsu, Earley, & Wolf, 2006; Mesterton-Gibbons, 1999; Rutte, Taborsky, & Brinkhof, 2006), or because residents have a physiological advantage granted by spending the time preceding the contest in a favourable territory (Kemp & Wiklund, 2001; Kemp & Wiklund, 2004). Residents may also have a physical advantage in the contest imbued by superior positioning (Fayed et al., 2008). Finally, in some cases residents may win because of an ownership convention, where the ownership of a territory is an arbitrary means to settle disputes between well-matched individuals, while avoiding costly confrontations (see Kokko et al., 2006; Smith, 1982; Smith & Parker, 1976).

While there are clear theoretical predictions for which factors ought to influence contest dynamics and outcomes in animals, all-out conflicts are rare in nature, and much of our knowledge about animal contests has therefore been gained through staged contests conducted in laboratory settings. However, staged contests in the laboratory may not reflect the full range of motivational effects that influence decision making in wild animals, and there is often not a good understanding of how various factors function in concert to influence contest dynamics and outcomes in naturalistic settings. Here, we investigate resource contests in wild individuals of the cooperatively breeding cichlid, *Neolamprologus pulcher*. These substrate-spawning cichlids are endemic to Lake Tanganyika, Africa, and are obligate cooperative breeders that live in permanent social groups composed of a single dominant breeding pair and up to 20 nonbreeding subordinates of both sexes that assist in the maintenance and defence of the group territory and may provide direct alloparental care (Balshine et al., 2001; Balshine-Earn, Neat, Reid, & Taborsky, 1998; Taborsky & Limberger, 1981; Wong &

Balshine, 2011). Each social group defends a permanent year-round territory within a larger *N. pulcher* colony in the rocky littoral zone (Taborsky & Limberger, 1981; Wong & Balshine, 2011). While females are philopatric and tend to ascend to breeding positions within their natal social groups, males tend to disperse and must compete to gain access to the dominant breeder position within a new social group (Dierkes, Heg, Taborsky, Skubic, & Achmann, 2005; Stiver, Fitzpatrick, Desjardins, & Balshine, 2006; Wong & Balshine, 2011). In the current study, we took advantage of the natural life history of these fish to elicit territorial conflicts between high-ranking male *N. pulcher*. We removed the 'original resident' dominant breeder male from a number of social groups and held these fish away from their territory for a period of time, during which a large 'usurper male' typically moved in. By releasing the original resident male back into his territory, we were able to reliably elicit an aggressive territorial conflict between the original resident and the usurping male.

We asked a series of questions with the aim of improving our understanding of the factors that influence contest dynamics and outcomes in wild fish. First, since body size is often an important predictor of contest dynamics (reviewed in Arnott & Elwood, 2009), including in *N. pulcher* (Reddon et al., 2011), we measured contestant body size and predicted that contests between well-matched individuals would take longer to resolve and contain more aggressive acts than mismatched contests. Furthermore, we predicted that as the relative size difference increased, the probability of the larger individual (i.e. the individual with greater RHP) winning should also increase. Resource value also strongly influences the level of aggression produced during contests, with animals being more willing to incur higher costs during a contest in order to acquire more valuable resources (reviewed in Arnott & Elwood, 2008). Therefore, to understand how objective resource value influences both original resident and usurper aggression, we measured social group size and breeder female size and used these as measures of objective resource value. Larger groups of *N. pulcher* produce more offspring, hold higher-quality territories with more shelters (Balshine et al., 2001) and are more likely to persist through time than smaller groups (Heg, Brouwer, Bachar, & Taborsky, 2005), while larger females have higher fecundity (Bagenal, 1978; Trivers, 1972). Thus, both larger groups and larger breeder females should be more valuable resources for *N. pulcher* males relative to smaller groups and smaller females. We predicted that both original residents and usurpers would be more aggressive in contests over larger social groups and larger breeder females (Arnott & Elwood, 2008). Resource value can also be subjective. As a measure of context-dependent resource value to the original resident, we determined the mating system of the original resident. The mating system in *N. pulcher* is flexible, and socially monogamous males defend a single territory containing a single breeding female, while socially polygynous males defend multiple territories, each containing a breeding female (Desjardins, Fitzpatrick, Stiver, Van Der Kraak, & Balshine, 2008; Wong et al., 2012). A sole territory will have higher subjective value than one with several territories (Arnott & Elwood, 2008), and so we predicted that original resident males with a single territory would defend their sole territory more aggressively when compared to original residents defending one of two or more territories. Finally, to manipulate subjective resource value for the usurper male, we removed some of the original resident males for a 'short' period (4.5 h), while we removed other original resident males for a 'long' period (20 h). We predicted that the usurping males would have increased residency times and become more familiar with the territory as the original male removal time increased. Based on previous studies investigating residency effects in fish (e.g. Figler & Einhorn, 1983; Johnsson, Nöbbelin, & Bohlin, 1999; Turner, 1994)

and other animals (reviewed in Kemp & Wiklund, 2004), we predicted that the usurping males would become more aggressive and more willing to engage in longer contests following the long removal period. Since more aggressive animals are also more likely to win contests (Parker, 1974; Parker & Stuart, 1976; Stuart-Fox, 2006), we further predicted that the more aggressive *N. pulcher*, arising from the factors described above, would be more likely to win contests.

METHODS

Study Site, Study Animals and Experimental Protocols

The study site was located at Kasakalawe Bay in southern Lake Tanganyika, Zambia (8°46'52"S, 31°5'18"E). This site is characterized by a mix of sand and cobble substrate and a gentle descent to depth (for detailed descriptions of the study site, see Balshine-Earn et al., 1998; Heg et al., 2005; Stiver, Dierkes, Taborsky, & Balshine, 2004, 2006; Wong et al., 2012). In March–April 2013, we located *N. pulcher* territories using SCUBA between depths of 9 and 12 m. Once a territory was identified, we observed the dominant breeder male for 15 min, following a protocol modified from Desjardins, Fitzpatrick, et al. (2008) and Wong et al. (2012). During this preliminary observation, we determined whether the male was socially monogamous or polygynous by observing whether he spent time in more than one territory. We determined the edges of each male's territory or territories based on the area the male defended against other conspecifics and heterospecifics. We then counted the number of conspecific territories within a 2 m radius of each territory and counted the number of subordinate fish on the territory, classifying them as 'small' (<3 cm in length), 'medium' (3–4 cm in length) or 'large' (>4 cm in length) based on an estimated size relative to a ruler. We also noted whether or not there were newly hatched juveniles within the territory. After this preliminary observation, we collected the dominant breeder male using a fence-net and a hand-net, measured the fish for standard length (SL, measured from the tip of the snout to the end of the caudal peduncle) to the nearest millimetre using a measuring tape, gave the fish a dorsal fin clip for identification and transferred him to an opaque, covered plastic bucket (~6-litre volume) outfitted with a series of holes to allow free water circulation. We firmly anchored these buckets to the substrate approximately 3–4 m from the territory. Fin clips were chosen for identification because fish recover immediately, behaviour is not affected by the procedure, and the clipped fin grows back in approximately 2 weeks (Stiver et al., 2004). Following the capture of the dominant breeder male, we measured the area of the dominant breeder male's territory or territories using a measuring tape and made a map that included the location and size of rocks within the territory or territories. The original resident males in the anchored plastic bucket were left for either a 'short' period (i.e. the period between a morning and afternoon dive; mean = 4.5 h, range 4.1–5.2 h) or a 'long' period (i.e. the overnight period between an afternoon and a morning dive; mean = 20.1 h, range 17.5–23.8 h). After the short or long removal period, the same observer who performed the preliminary observations returned, transferred the original resident breeder male to a presentation chamber (a clear plastic drawer measuring 10 × 18 × 30 cm) using a hand-net and placed the presentation chamber in the centre of the territory. For socially polygynous males, the chamber was placed in the centre of the territory where the male had spent the most time during the preliminary observation. We placed the original resident males in a presentation chamber rather than simply releasing them on the territory so that the original male could orient himself within the

territory and the colony prior to being released. After a 10 min acclimation period within the presentation chamber, we carefully released the original resident from the transparent presentation chamber by sliding the drawer out of the plastic sleeve and allowing the fish to swim out of the container. Animals were never chased or otherwise coerced to leave the presentation chamber, and all males left the presentation chamber within a few seconds. We then observed and live-scored all behavioural interactions between the original resident and the usurping male. We continued to live-score all behavioural interactions for up to 10 min, or until one fish was successfully chased from the territory, at which point the observation was terminated so that the observer could catch the usurper. Both the usurper male and the breeder female on the territory were captured using a fence-net and a hand-net, measured for SL and released at their capture site.

Behavioural scoring

Behaviours were scored based on a published ethogram for resource contests in *N. pulcher* (Hick, Reddon, O'Connor, & Balshine, 2014). Behaviours observed were aggressive displays, including aggressive postures (focal fish lowers its head and raises its tail in front of its opponent), frontal displays (also called a puffed throat or an opercular flare, the focal fish extends its opercula and lower jaw), head shakes (focal fish thrashes its head from left to right repeatedly) and pseudo mouth wrestles (both fish rapidly move back and forth with open mouths while facing each other, as if about to mouth wrestle, but no physical contact is established; see description of mouth wrestle below), as well as overt physical attacks, including chases (the focal fish darts quickly towards its opponent), rams (focal fish makes contact with another fish using the head or mouth region, but no obvious bite is taken and jaws remain closed), bites (focal fish bites its opponent) and mouth wrestles (also known as a mouth fight; focal fish and its opponent lock jaws and push against one another in a reverse tug of war). Mouth wrestles represent a highly escalated phase of a cichlid contest, involving considerable expenditure of energy, reduced attention to predators and heightened injury risk (Brick, 1998; Enquist & Jakobsson, 1986; Enquist et al., 1990; Koops & Grant, 1993; Neat, Taylor, & Huntingford, 1998). Therefore, mouth wrestles are an important indicator of contest cost in cichlids (Brick, 1998). We recorded both the number of mouth wrestles and the duration of each mouth-wrestling bout. Finally, we recorded the total duration of the contest. The start of the contest was considered the first aggressive act from either fish after the release of the original resident from the presentation chamber. The end of the contest was recorded when the winning fish vigorously chased the losing fish away from the territory, which occurred in every contest.

Statistical Analyses

All statistics were performed in R version 3.0.2 (R Development Core Team, 2013) within R Studio version 0.98.501 (RStudio, 2013). The level of significance for all tests was assessed at $\alpha = 0.05$.

Description of the contest

First, we separately summed the total number of aggressive displays (aggressive postures, frontal displays, head shakes and pseudo-mouth wrestles) and the total number of overt physical attacks (chases, rams and bites) for the original resident and for the usurper male. To understand the structure of the contest, we then calculated the average rate of displays per minute and the average rate of physical attacks per minute. Finally, we calculated the average contest duration, the average number of mouth wrestles

and the average mouth-wrestling duration. As a preliminary examination of how contests in the field might differ from laboratory-based contests, we compared these to published laboratory accounts of resource contests in *N. pulcher* (Reddon et al., 2011) using Student's *t* tests.

What factors influence contest behaviour?

We wanted to explore the influence of the relative competitive ability and measures of objective and subjective resource value on resource contest dynamics in wild male *N. pulcher*. We therefore explored the effects of the relative percentage size difference between the contesting males, the social group size, resident female body size, original resident male mating system and original resident male removal time on (1) total aggression of the original resident and the usurper male during the contest, (2) the number of mouth-wrestling bouts, (3) the total mouth-wrestling duration and (4) the total contest duration. We calculated the relative percentage size difference between the males as $((\text{original resident SL} - \text{usurper SL}) / ((\text{original resident SL} + \text{usurper SL}) / 2)) \times 100$. Thus, positive values indicate that the original resident is larger and negative values indicate that the usurper is larger, and we used these signed values for models testing total aggression of the original resident and usurper. Since we predicted that the number of mouth-wrestling bouts, the total mouth-wrestling duration and the total contest duration would be longer for well-matched fish, regardless of which fish was larger, in these models we used the absolute value of the size difference, such that all values were positive regardless of which fish was larger. To explore these relationships, we used generalized linear models with negative binomial distributions and log-link functions (negative binomial GLMs), appropriate for overdispersed count data (Bolker, 2008; Zurr et al., 2013). We tested overdispersion using the AER package (Kleiber & Zeileis, 2008) to determine whether the negative binomial was an appropriate distribution and ran the GLMs using the MASS package (Ripley et al., 2014).

What factors are related to contest outcome?

We used a binomial test to determine whether original residents or usurpers won contests more often. To determine what factors contributed to contest outcome, we ran a multiple logistic regression model using the base package in R with winner (original resident or usurper) as the outcome and the relative size difference between the males, social group size, resident female body size, original resident male mating system and original resident male removal time as predictor variables. Since more aggressive animals are more likely to win contests (Parker, 1974; Parker & Stuart, 1976; Stuart-Fox, 2006), we also evaluated whether original resident and usurper male total aggression predicted the contest winner, using a separate multiple logistic regression model in order to avoid autocorrelation among the independent variables.

Ethical Note

During all procedures, we took care to minimize handling time and stress as much as possible for the study animals. We observed no visible injuries during the contests. *Neolamprologus pulcher* are neither endangered nor threatened. The methods described for animal capture, housing, marking and treatments were assessed and approved by the Animal Research Ethics Board of McMaster University (Animal Utilization Protocol No. 10-11-71) and adhered to both Canadian and Zambian laws, as well as the guidelines of the Canadian Council for Animal Care and the Animal Behavior Society/ Association for the Study of Animal Behaviour.

RESULTS

Description of the Contest

In total, we attempted 59 short removals and 18 long removals. Because of time constraints at the end of the field season, we were not able to balance the sample sizes for the two treatments. Of these, 21 short removals (35% of the attempted trials) and 11 long removals (61% of the attempted trials) resulted in a territorial contest between the original resident and a usurping male that took over the territory while the original resident breeder male was removed. Of the failed trials, 11 of the short removal trials (19% of the attempted short removal trials) and two of the long removal trials (11% of the attempted long removal trials) failed because no usurping male took over the territory while the original resident breeder male was removed, and so the original resident was able to return to the territory without conflict. The remaining 27 short removal attempts (45% of the attempted short removal trials) and five long removal trials (28% of the attempted long removal trials) failed because the original resident fled from the territory without engaging with the usurping male.

Excluding the trials that failed because no usurping male took over the territory, there was not a significant difference between short and long removals in the ratio of trials where the original resident fled to trials where an escalated contest occurred (Fisher's exact test: $N = 64$, $P = 0.15$). We could not definitively determine why the original residents fled without engaging the usurping male in these cases, and we were concerned that effects of handling or confinement may have influenced the original residents to flee rather than engage in a contest. Therefore, to be conservative, for all subsequent analyses we included only the 21 short removals and 11 long removals that resulted in territorial conflicts between the original resident and a usurper male, since all of these fish demonstrated the threshold level of motivation to engage in a contest. Interestingly, subordinate males within the territory never attempted to engage the returning original resident in a territorial contest upon his return, and so all successful contests were between original residents and usurping males from outside the territory.

We found that these 32 contests between wild free-swimming males were significantly shorter and more intense than those previously reported for *N. pulcher* in the laboratory (Table 1). The average contest duration was about 2 min and involved an average of 13 aggressive acts/min, with eight of these aggressive acts being physical attacks (Table 1).

What Factors Influence Contest Behaviour?

In the 32 successful contests, the mean \pm SE standard length of original resident males was 62.0 ± 0.6 mm (range 56–70 mm; Fig. 1a) while usurpers were on average 61.3 ± 0.8 mm in SL (range 51–69 mm; Fig. 1a). Males were well matched in these contests, with the mean \pm SE standard length of the original resident males being $1 \pm 0.01\%$ larger than that of the usurper males. The size differences ranged from a case where the original resident male was 18% larger than the usurper male, to a case where the original resident male was 11% smaller than the usurper male (Fig. 1b), and there was no consistent size difference between the males (paired *t* test: $t_{30} = 0.95$, $P = 0.35$). Surprisingly, there was no effect of the relative size difference between the usurper and the original resident on the original resident's or usurper's rate of aggression during the contests (Table 2). There was similarly no effect of the absolute value of the relative size difference between the two males in the contest on the number of mouth wrestles, mouth-wrestling duration or total contest duration (Table 2, Fig. 2).

Table 1

Comparison of a previously published account of *Neolamprologus pulcher* contests in the laboratory (Reddon et al., 2011; $N = 45$) and the current account of contests between wild male *N. pulcher* in the field ($N = 32$)

Variable	Lab-based contests	Field-based contests	<i>t</i>	<i>df</i>	<i>P</i>
Contest duration (s)	578±45 (85–1194)	125±15 (15–335)	8.25	75	<0.001
Aggressive acts/min	5.6±0.4 (1.4–13.3)	12.8±1.6 (2.7–36.0)	5.05	75	<0.001
Displays/min	4.4±0.3 (0.9–11.0)	5.3±0.7 (0–18)	1.31	75	0.19
Physically aggressive acts/min	1.6±0.2 (0–8.8)	7.5±1.2 (1.4–28)	5.69	75	<0.001

Values are means ± SE, with ranges in parentheses. Significant differences between the laboratory-based and field-based contests as determined by Student's *t* tests are indicated in bold ($\alpha = 0.05$). See Methods for full statistical details.

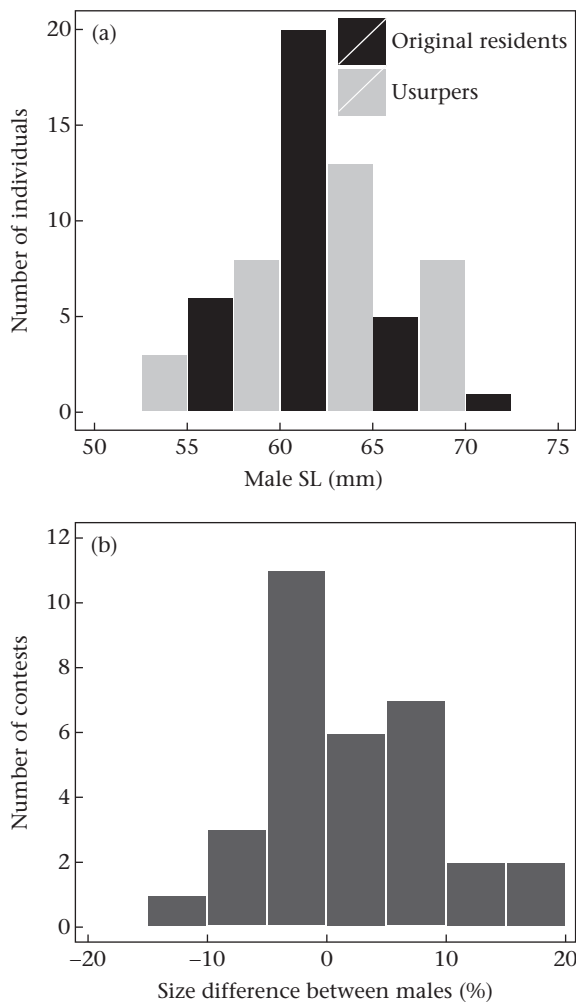


Figure 1. (a) Size range (standard length, SL) of *Neolamprologus pulcher* resident and usurper males in the current study. (b) Relative size difference between the original residents and the usurper males. Positive values indicate contests where original residents were larger than the usurper males, and negative values indicate contests where usurpers were larger than the original resident males.

We examined the potential effects of objective and subjective resource value on contest dynamics by assessing the effects of social group size, resident female size, original resident removal time and social mating system of the original resident. We found that long removal periods resulted in higher rates of usurper aggression (Table 2, Fig. 3a), more mouth wrestles (Table 2, Fig. 3b), longer average mouth-wrestling duration (Table 2, Fig. 3c) and longer overall contests (Table 2, Fig. 3d). Socially monogamous original residents also displayed higher rates of aggression (Table 2, Fig. 4). However, neither of the objective measures of resource value (i.e. social group size or resident female size) significantly influenced contest dynamics (Table 2).

What Factors Are Related to Contest Outcome?

Usurpers won contests more frequently than the original resident, with 24 contests (9 long removals, 15 short removals) being won by usurper males and eight contests (2 long removals, 6 short removals) being won by the original residents (binomial test of the difference from an expected ratio of 0.5: $N = 32$, $P = 0.007$). Contests won by the original residents were characterized by high rates of aggression by the original resident (Table 3) and low rates of aggression by the usurper (Table 3). Neither the relative size difference between the males nor the measures of objective and subjective resource value predicted contest outcome (Table 3).

DISCUSSION

In wild free-swimming cichlid fish, we found little evidence that relative resource-holding potential (RHP) influences contest dynamics or outcome, probably because the males in this study were all relatively large and contests were well matched. Instead, we found strong support for subjective resource value being the primary driver of contest dynamics in wild male *N. pulcher*, and the only factor that directly predicted contest outcome was the level of aggression displayed by each male.

Field Contests Are Shorter and More Intense Than Laboratory Contests

In terms of basic contest dynamics, we found that the contests that we observed in the field were shorter and more intense than those previously described for *N. pulcher* in the laboratory (Hick et al., 2014; Reddon et al., 2011). These differences in contest dynamics may be based on differences in status and contest experience between the fish included in the previous laboratory studies relative to the fish included in the current field study. Reproductive opportunities have a strong effect on aggression (e.g. Brown, Chimenti, & Siebert, 2007), and although individuals in the laboratory contests and field contests were similar in size (size range of 56–70 mm in the current study and 42–70 mm in the laboratory study; Reddon et al., 2011), the fish in the laboratory study had never reproduced. Conversely, all of the fish in the current study were territory-holding males, or males attempting to gain a territory, and were presumably highly motivated by the reproductive opportunities offered by winning the contest. Prior winning experience also increases the willingness of animals to engage in contests (Hsu et al., 2006) and, at least the original residents, if not all of the fish, involved in the current field study had probably won contests prior to our staged conflicts in order to secure and maintain their status as dominant breeding males. In addition to differences in status and contest experience, the difference in contest dynamics might be based on differences in aggression between wild and laboratory-reared fish. For example, hatchery-reared salmonids are more aggressive than wild salmonids (McMichael, Pearsons, & Leider, 1999; Swain & Riddell, 1990), and it is

Table 2
Results of generalized linear models, with negative binomial error distributions and log-link functions, exploring factors that influence contest dynamics in wild male *Neolamprologus pulcher*

Dependent variable	Independent variables	Estimate	SE	df	z	P
Original resident aggression	Relative size difference between males	0.21	0.27	26	0.78	0.44
	Removal time (short vs long)	0.36	0.27	26	-1.31	0.19
	Original resident male mating system	-0.78	0.26	26	-3.00	0.003
	Social group size	-0.17	0.25	26	-0.69	0.49
	Breeder female size	-0.22	0.26	26	-1.84	0.40
Usurper aggression	Relative size difference between males	0.19	0.23	26	0.81	0.42
	Removal time (short vs long)	0.68	0.23	26	-2.98	0.003
	Original resident male mating system	-0.20	0.22	26	-0.93	0.35
	Social group size	-0.01	0.21	26	-0.06	0.95
	Breeder female size	-0.18	0.22	26	-0.85	0.40
Mouth wrestles	Relative size difference between males	0.53	0.50	26	0.07	0.28
	Removal time (short vs long)	1.23	0.45	26	-2.72	0.007
	Original resident male mating system	0.27	0.43	26	0.62	0.54
	Social group size	-0.30	0.42	26	-0.71	0.48
	Breeder female size	0.27	0.42	26	0.64	0.52
Mouth-wrestling duration	Relative size difference between males	-0.50	0.89	26	-0.56	0.58
	Removal time (short vs long)	1.96	0.91	26	-2.17	0.03
	Original resident male mating system	0.42	0.85	26	0.50	0.62
	Social group size	0.57	0.81	26	0.71	0.48
	Breeder female size	-0.57	0.85	26	-0.67	0.50
Contest duration	Relative size difference between males	0.27	0.26	26	1.02	0.31
	Removal time (short vs long)	0.76	0.27	26	2.85	0.004
	Original resident male mating system	-0.16	0.25	26	-0.64	0.52
	Social group size	0.22	0.24	26	0.94	0.35
	Breeder female size	-0.12	0.23	26	-0.48	0.63

We explored the potential effects of relative resource-holding potential (RHP, measured here as the percentage difference in standard length), objective resource value (social group size, resident female size) and subjective resource value (original resident mating system, removal time) on contest dynamics during 32 territorial contests. Significant terms are indicated in bold ($\alpha = 0.05$). See [Methods](#) for full statistical details.

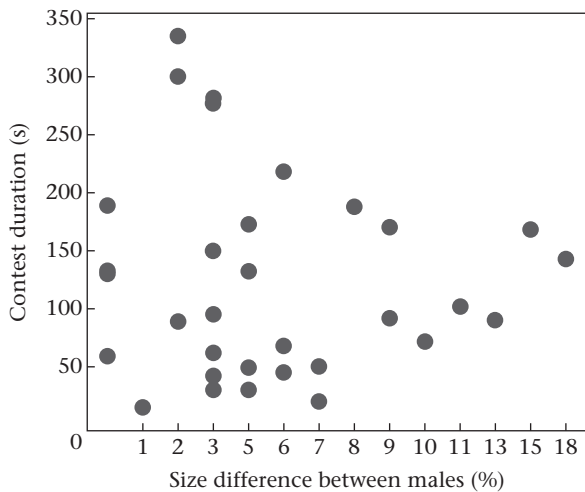


Figure 2. Influence of the relative size difference between contestants on contest duration in wild male *Neolamprologus pulcher*. Here, the absolute value of the percentage difference in standard length (SL) is presented. Small values indicate males that were similar in size, while large values indicate mismatched contests.

possible that differences also arise (although in the opposite direction) between wild and laboratory-reared *N. pulcher*, based on factors such as food availability and typical rates of space competition. There is also a risk of predation during and after contests in the field, which does not exist for laboratory fish. This difference might explain both the increased contest intensity (i.e. an increased motivation to secure a territory) and the decreased contest duration (i.e. an increased motivation to resolve a contest rapidly in order to reduce the time spent engaged in a risky contest) in field-based contests relative to laboratory-based contests.

Furthermore, fish contesting in a laboratory setting are restricted to a relatively small aquarium and are familiar with being housed in aquaria with other similarly sized fish. In this context, fish are likely to contest to form dominance hierarchies, rather than to entirely oust their opponent. For example, [Hick et al. \(2014\)](#) showed that *N. pulcher* use submissive displays during laboratory contests to establish dominance hierarchies. In the field-based contests, the fish are free to engage in the contest or flee entirely from the conflict. Since these are contests between dominant breeding males, these males are also unlikely to remain in the same social group and have less shared interest in resolving the contest at a low cost through behaviours like submissive displays rather than fleeing ([Matsumura & Hayden, 2006](#); [Ligon, 2014](#); [Reddon & Reader, n.d.](#)). Accordingly, in the current study, we saw no submissive displays produced by any of these large, dominant male fish. Conducting basic aggression assays with fish of similar status in the laboratory and field, or conducting repeated staged conflicts using breeding males in the laboratory, would both be useful future directions. Both assays would help reveal whether the differences that we found between prior laboratory studies and the current field study are experience or status driven, whether fish in the field are more aggressive than fish in the laboratory, or if a combination of these factors influences contest dynamics.

Subjective Resource Value and Contest Dynamics

We found that socially monogamous original residents, contesting over their sole territory, were more aggressive than socially polygynous original residents, contesting over one of several territories. This result was consistent with our predictions, based on the subjective value of the territory to the original resident males. In their review of the influence of resource value in animal contests, [Arnott and Elwood \(2008\)](#) pointed out that subjective resource

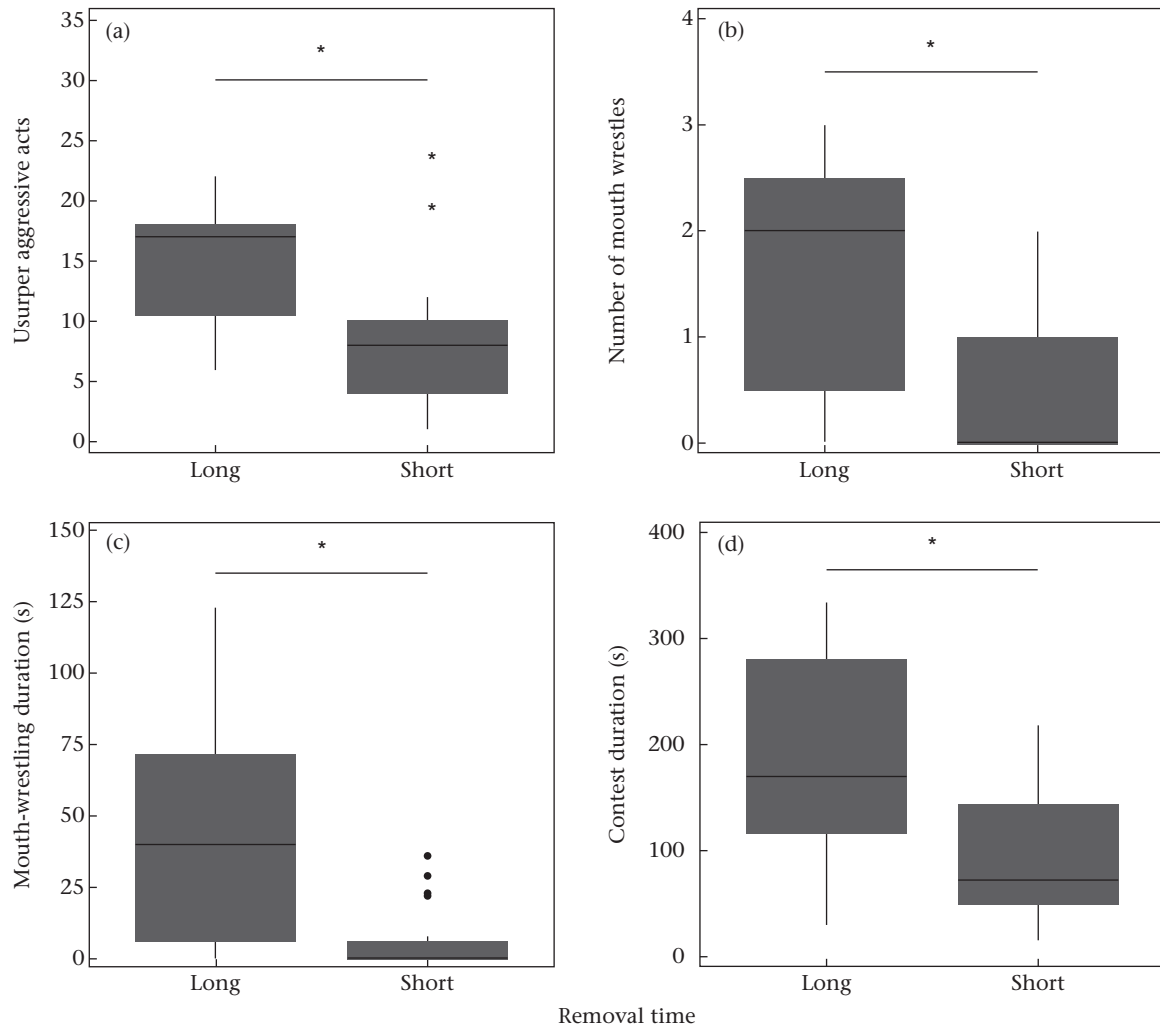


Figure 3. Box plots of the (a) number of aggressive acts by usurpers, (b) number of mouth wrestles, (c) mouth-wrestling duration and (d) contest duration during contests between resident breeder male *Neolamprologus pulcher* and usurping males following temporary removal of residents for short (4.5 h) and long (20 h) periods. Box plots show medians (lines in the boxes), 25% and 75% quartiles (boxes), outermost values within the range of 1.5 times the respective quartiles (whiskers) and outliers (circles). Asterisks indicate significant differences ($\alpha = 0.05$). See [Methods](#) and [Table 2](#) for full statistical details.

value is often an important predictor of contest dynamics and outcome. For example, hungry individuals are more aggressive and more likely to be successful in contests over food resources than satiated individuals in a range of insects (Crowley et al., 1988; Nosil, 2002) and birds (Cristol, 1992; Hansen, 1986; Popp, 1987; Rodríguez-Girones et al., 1996). Similarly, male house crickets, *Acheta domesticus*, that have not mated recently are also more aggressive and more likely to win contests over females than males with consistent exposure to females (Brown et al., 2007). Our results therefore contribute to an increasing body of literature emphasizing the importance of internal motivation and subjective resource value in dictating the dynamics and outcomes of animal contests.

As expected, we found that more aggressive fish were more likely to win contests (Parker, 1974; Parker & Stuart, 1976; Stuart-Fox, 2006) and that socially monogamous males were more aggressive than polygynous males. However, we did not find that social mating system directly predicted fight outcome. This is probably because we had only eight contests where the original resident male won, and therefore, were limited in our power to identify the factors that influence contest outcome. We should also note that in our study, we also used a single 15 min observation

period to classify mating system, while previous studies have used 'two or three 5 min observation periods' to classify *N. pulcher* males as either socially monogamous or polygynous (Desjardins, Fitzpatrick, et al., 2008; Wong et al., 2012). Thus, the total duration of our observation period is consistent with previous studies, but we visited the males only once, and it is possible that some polygynous original residents were falsely identified as monogamous during our study. However, this potential bias would support the null hypothesis, and if anything, the true effect of social mating system on original resident contest motivation is likely stronger than the effect documented in our study.

Also as predicted, we found that longer removal times increased the rates of aggression from the usurping male as well as the number and duration of mouth wrestles and the total contest duration. There are two potential confounds that may have contributed to the strong effect of removal time. First, all of the long removal contests occurred in the morning, while all of the short removal contests occurred in the afternoon, so it is possible that the effects of removal treatment are partially confounded by circadian effects. *Neolamprologus pulcher* feed at higher rates in the morning than in the afternoon (Desjardins, Fitzpatrick, Stiver, Van Der Kraak, & Balshine, 2011), and it is conceivable that fish are more active

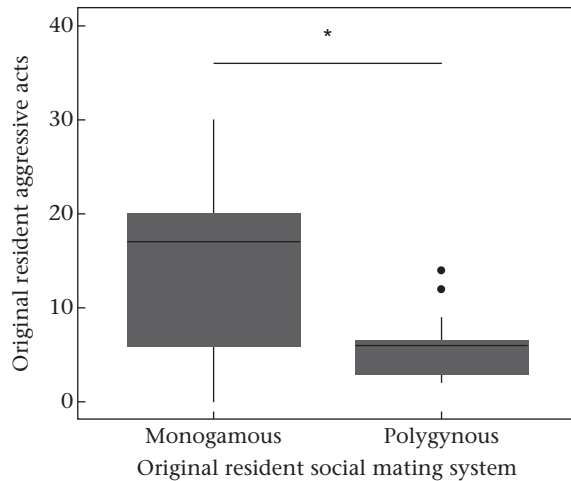


Figure 4. Influence of original resident breeder male social mating system on contest dynamics in wild male *Neolamprologus pulcher*. Socially monogamous: males defending a single territory; socially polygynous: males defending one of at least two territories. Box plots show medians (lines in the boxes), 25% and 75% quartiles (boxes), outermost values within the range of 1.5 times the respective quartiles (whiskers) and outliers (circles). Asterisks indicate significant differences ($\alpha = 0.05$). See [Methods](#) and [Table 2](#) for full statistical details.

Table 3

Results of logistic regression models exploring factors that influence contest outcome in wild male *Neolamprologus pulcher*

Independent variables	Estimate	SE	df	t	P
Original resident aggression	1.24	0.26	29	4.75	<0.001
Usurper aggression	-0.86	0.24	29	-3.55	0.002
Relative size difference between males	0.19	0.15	26	1.29	0.21
Removal time (short vs long)	0.22	0.18	26	1.20	0.24
Original resident male mating system	0.29	0.17	26	1.65	0.11
Social group size	0.10	0.14	26	0.70	0.49
Breeder female size	-0.03	0.14	26	-0.21	0.83

We explored the potential effects of male aggression, relative resource-holding potential (RHP, measured here as the percentage difference in standard length), objective resource value (social group size, resident female size) and subjective resource value (original resident mating system, removal time) on contest outcome during 32 territorial contests. Significant terms are indicated in bold ($\alpha = 0.05$). See [Methods](#) for full statistical details.

overall in the morning and therefore more willing to engage in escalated contests. However, given that usurpers, but not original residents, were more aggressive following the long removal treatment relative to the short removal treatment, circadian effects are unlikely to entirely account for our results. Nevertheless, future studies controlling for circadian effects in *N. pulcher* would be very useful in disentangling any potential effects of time of day on contest dynamics. Second, it is possible that the longer holding time associated with the long removal allowed the original residents to fully recover following the capture stress (e.g. fish can take up to 6 h to recover following capture by rod and reel; [Cooke, Schreier, Wahl, & Philipp, 2002](#)), or that the isolation for 20 h increased the level of aggression in the original residents (e.g. [Earley et al., 2006](#)). However, since removal time not affect contest outcome and did not affect whether the original residents engaged the usurpers or displayed aggression during the contests, any potential effects of holding time on the original resident were probably relatively minor in the greater context of the study. Overall, the most likely explanation for the increased aggression, and in particular the increased aggression of the usurper, following the long removal is that longer residency times are typically associated with greater motivation to defend the territory (e.g. [Figler & Einhorn, 1983](#);

[Johnsson et al., 1999](#); [Turner, 1994](#)). Although we do not know when the usurpers moved into the territories, it is likely that the longer removal period in our study increased residency time for the usurpers and gave them a greater sense of territory ownership. Longer residency times probably meant that the usurping males devoted more time and energy exploring the territory, overcoming potential resistance from the current social group members, settling disputes with neighbours and other territorial contenders, and otherwise became increasingly invested in the territory. The strong effect of removal time on contest dynamics, combined with the effect of original resident social mating system on original resident aggression, emphasizes that subjective resource value plays a large role in dictating the costs that *N. pulcher* males are willing to pay during territorial contests.

Objective Resource Value and Contest Dynamics

Contrary to our predictions, neither social group size nor female body size influenced the level of aggression displayed by the original resident or the usurping male. Although theoretical models predict that individuals should be willing to incur more costs for higher-quality resources ([Enquist & Leimar, 1987](#); [Hammerstein & Parker, 1982](#)), previous research has shown that some species do not assess resource value during contests. As reviewed in [Arnott and Elwood \(2008\)](#), there are examples from insects ([Englund & Olsson, 1990](#); [Goubault et al., 2007](#); [Jakob, 1994](#); [Thornhill, 1984](#)), fish ([Keeley & Grant, 1993](#); [Lindström, 1992](#)) and mammals ([Jennings et al., 2004](#)) where individuals fight with equal vigour over low- and high-quality resources. Interestingly, in parasitoid wasps (*Goniozus nephantidis*), resource value does not influence fight outcome during owner–intruder contests, but becomes a predictor of contest outcome when ownership status is controlled ([Humphries, Hebblethwaite, Batchelor, & Hardy, 2006](#)). Similarly, our results suggest that *N. pulcher* males do not assess territory quality during territorial contests or that motivational factors override assessment of territory quality in some circumstances.

There are two potential confounds that limit our ability to draw strong conclusions regarding the assessment of territory quality. First, territories of socially monogamous *N. pulcher* males tend to be of higher quality than those of socially polygynous males ([Desjardins, Fitzpatrick, et al., 2008](#)), so the strong effect of social mating system may have masked more subtle effects of social group size or female body size on the original resident's behaviour in our study. Second, we had relatively low variation in territory quality among trials, so it is possible that either a larger sample size or a sample that included a larger variance in territory quality might be necessary to detect differences in contest behaviour based on objective resource value. Future studies that include a wider range of resource value or experiments that manipulate resource value would be valuable to identify whether *N. pulcher* males assess territorial quality during resource contests and how this weighs into their decision-making process during contests.

The Implications of Well-matched Males

Body size is strongly correlated with dominance hierarchy structure in *N. pulcher* ([Dey, Reddon, O'Connor, & Balshine, 2013](#); [Fitzpatrick et al., 2008](#); [Hamilton, Heg, & Bender, 2005](#); [Heg, Bender, & Hamilton, 2004](#); [Werner, Balshine-Earn, Leach, & Lotem, 2003](#)). However, we found little evidence in the current study that body size influences contest dynamics or outcome for wild dominant male fish engaged in territorial conflicts. This lack of an effect is likely due to the highly constrained size range of the dominant male fish contesting in our current study. Most of the contests in the current study involved males that were within 5% of

each other's body size (SL), which is too small a difference for contest outcomes to be predicted a priori in this species in the laboratory (Reddon et al., 2011). Therefore, while RHP contributes to overall dominance structures (Dey et al., 2013; Fitzpatrick et al., 2008; Hamilton et al., 2005; Heg et al., 2004), relative RHP may be less important in escalated contests between large breeder males, perhaps due to a ceiling effect in body size for the most dominant males in the population.

Almost all of the contests in the current study involved males that were well matched in terms of body size, and the original residents were no larger than the usurping males. If the dominant original residents in our study were indeed the largest males in the population, with the highest RHP, then we would expect presumably smaller usurpers to attempt to take over territories opportunistically once the original residents were removed. Instead, resident and usurper males were similar in size, and in some cases, the usurping males were larger than the original resident. In some cases, we recognized the usurping male as a dominant breeding male from a nearby social group (i.e. a neighbouring dominant male), who opportunistically expanded his holdings following removal of the original resident. In other cases, it was unclear whether the usurping male was a more distant neighbour or a 'floater' without a territory of his own. In either case, it is interesting that even the larger usurping males did not take over the territory of a smaller original resident until we perturbed the system and temporarily removed the original resident. These patterns raise an important question and perhaps reveal insight into some of the factors that govern colony formation in *N. pulcher*. If many of the largest males in the population have similar resource-holding potential, what keeps the peace within the colony?

The remarkable consistency in the size of original residents and usurpers suggests that *N. pulcher* colonies are governed by strong respect for ownership. Game theory models suggest that ownership respect could function as an arbitrary means to settle disputes between well-matched individuals, while avoiding costly confrontations (Kokko et al., 2006; Smith, 1982; Smith & Parker, 1976). Others have suggested that ownership conventions need not be arbitrary, but may arise because the territory owners place greater value on the resource (Johnsson & Forser, 2002; Krebs, 1982), because of the self-reinforcing effects of prior winning experience (Earley et al., 2013; Goubault & Decuignière, 2012; Hsu et al., 2006; Mesterton-Gibbons, 1999; Rutte et al., 2006), or because residents have some kind of physiological (Kemp & Wiklund, 2001; Kemp & Wiklund, 2004) or mechanical (Fayad et al., 2008) advantage. For example, in juvenile brown trout, *Salmo trutta*, a 30% difference in size is necessary to overcome a residency advantage (Johnsson et al., 1999). Given that all of our males were within 30% of each other in body size, it is possible that potential usurper males are rarely, if ever, sufficiently large to overcome the strong residency advantage held by the dominant resident males in natural, unperturbed groups. Without the removal that we performed, it is possible that none of the usurper males would have attempted to take over the original residents' territories. High rates of predation likely contribute to a 'waiting game' approach for territorial take-overs in *N. pulcher*, both because fighting is costly and because vacancies are expected to regularly arise in the colony due to predation events. A social system therefore emerges where it is often not worth attempting a territorial take-over unless the previous resident has been removed, as would occur during a natural predation event, and was simulated by our experimental manipulation.

Conclusion

Overall, our study offers a rare window into the factors driving male aggression in the wild. Our results reveal a social system

where the largest males in the colony are typically well matched with each other in terms of body size and contest dynamics between these males are driven by motivational factors such as ownership conventions and prior residency effects, rather than by asymmetries in fighting ability.

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