



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)

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