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Original Article

Applying Lanchester's laws to the interspecific competition of coral reef fish

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Lanchester's laws of combat are a mathematical framework describing the relative contributions of individual fighting ability and group size to overall group fighting ability. Since 1993, several studies have attempted to apply this framework to interspecific dominance relationships between nonhuman animals. However, this prior work addressed only the corollaries of Lanchester's laws rather than the laws themselves. Here, we directly test Lanchester's linear and square law to explain interspecific competition of coral reef fish. First, we analyzed the relationship between body size and dominance to find a biologically accurate proxy of individual fighting ability. We then tested whether group fighting ability was linearly (linear law) or quadratically (square law) related to group size while accounting for the different fighting abilities of competing species. We found support for the linear law; however, both laws were outperformed by a simpler model that only included body size. After accounting for possible outliers and data limitations, we suggest that Lanchester's linear law may prove useful for explaining interspecific competition in marine ecosystems.

Key words: **coral reef fish, dominance hierarchy, interspecific competition, Lanchester's laws.**

INTRODUCTION

Dominance hierarchies established by interspecific competition play an essential role in determining community structure and composition (Putman and Wratten 1984). Variables such as body size, sex, territory ownership, and relative numbers influence these hierarchies (Fisler 1977; Cooper 1991; Johnsson et al. 1999; Lehmann et al. 2017), but their relative importance varies across species, making the search for general underlying principles difficult.

Although there is a rich ecological literature studying both intraspecific and interspecific competition (Connell 1983; Fausch 1998; Hansen et al. 1999; Price and Kirkpatrick 2009; Bolnick et al. 2010; Dhondt 2012; Louhi et al. 2014), extensive research has also been conducted on human warfare, and the 2 literatures are reciprocally illuminating (Franks and Partridge 1993; Aureli et al. 2006). During World War I, the British engineer Frederick Lanchester proposed a series of simple mathematical models to explain the relationship between the size of an army and its combat success. As a simplifying assumption, Lanchester (1916) treated all wars as wars of attrition, in which the winning army is always the one with the last man standing. He then focused on the rates of attrition of both sides.

For situations in which a spatial concentration of forces is impossible or unlikely to determine the outcome, a battle of armies M and N can be described by the following state equation:

$$\alpha_m (m - m_0) = \alpha_n (n - n_0), \tag{1}$$

where m_0 and n_0 are the initial sizes of armies M and N, respectively; m and n are their sizes at a given time; and α_m and α_n are the possibly unequal individual fighting abilities of their soldiers (notation following Adams and Mesterton-Gibbons 2003). Accordingly, army M wins over army N when

$$\alpha_m m \;> \alpha_n n. \tag{2}$$

Since the group fighting ability of each army is a linear function of its size, this inequality is commonly referred to as Lanchester's linear law. In behavioral ecology, the linear law has been understood as applying particularly or exclusively to one-on-one interactions (Whitehouse and Jaffe 1996; McGlynn 2000; Shelley et al. 2004). However, the connection between the linear law and one-on-one combat was first made by Franks and Partridge (1993) rather than by Lanchester (1916), who had originally derived his linear law from a different mechanistic model (Adams and Mesterton-Gibbons 2003). The attrition rate is different in this model (Adams and Mesterton-Gibbons 2003), but the state equation derived from integrating the attrition rate (Equation 1) is identical in both cases; the equivalency of the 2 scenarios was in fact noted by Lanchester (1916), p. 52.

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When it is possible to conduct concentrated attacks, each soldier in 1 army can become the target of more than 1 soldier from the opposing army. The effect of group size is amplified, and the attrition rates are described by the following set of equations:

$$\frac{dm}{dt} = -\alpha_n n, \tag{3}$$

$$\frac{dn}{dt} = -\alpha_m m. \tag{4}$$

Dividing 1 equation by the other and integrating the result yield a state equation of the form:

$$\alpha_m \left(m^2 - m_0^2\right) = \alpha_n \left(n^2 - n_0^2\right), \tag{5}$$

from which it follows that army M wins over army N when the following inequality is satisfied:

$$\alpha_m m^2 > \alpha_n n^2, \tag{6}$$

This relationship is generally known as Lanchester's square law.

In the first application of Lanchester's laws to ecology, Franks and Partridge (1993) equated the individual fighting abilities α_m, α_n with average body sizes. Whitehouse and Jaffe (1996) accepted this assumption, interpreting the linear law as stating that few large fighters can defeat a large number of small fighters, and the square law as predicting the opposite outcome (i.e., many small fighters can defeat few large fighters). Note, however, that both scenarios are compatible with either law as long as the difference between α_m and α_n is sufficiently large, or the difference between m and n is sufficiently small.

McGlynn (2000) introduced a further innovation by applying the linear law to contests in which a single individual from one body size guild competes against a single individual from another size guild. This is equivalent to setting m and n equal to 1, in which case Equation 2 reduces to

$$\alpha_m > \alpha_n, \tag{7}$$

and the outcome becomes solely a function of individual fighting ability. However, when $m = n = 1$, the square law (Equation 6) also reduces to the same inequality, and the 2 models become indistinguishable. Therefore, it is in principle impossible to test the validity of the linear law using one-on-one interactions only. Nevertheless, in focusing on one-on-one combat, McGlynn (2000) attempted to address an important question that had not received sufficient attention in the earlier studies: how does the individual fighting ability α relate to body size?

Another innovation introduced by McGlynn (2000) was the notion that Lanchester's laws could be applied even to nonlethal interactions that do not involve gradual elimination of the competing group, unlike the military contests modeled by Lanchester (1916) or the ant battles studied by Franks and Partridge (1993) and Whitehouse and Jaffe (1996). Given that combat at the broadest level involves not only killing, but also disabling or displacing opponents, Lanchester's laws are arguably relevant even to these latter cases. Functionally, attrition can be achieved by any of the 3 mechanisms, since all ensure that there are no combatants left. Thus, the ability of Lanchester's laws to predict the outcomes of nonlethal competitive interactions remains an open empirical question.

Shelley et al. (2004) revisited the question of a link between α and body size but made the incorrect assumption that a linear relationship between the 2 variables confirms Lanchester's linear law. In fact, the linear law refers to a linear relationship between overall group fighting ability and group size (m, n), and its validity does not depend on the manner in which the individual fighting abilities α_m and α_n are determined. Relationships that may exist between individual fighting ability and other biologically relevant quantities, such as body size or aggressiveness, can neither corroborate nor refute Lanchester's linear model. Moreover, like McGlynn (2000), Shelley et al. (2004) attempted to test the hypothesis of a linear relationship between body size and individual fighting ability using a nonparametric rank correlation technique that assesses monotonicity rather than linearity. Both studies found that individual fighting ability increases with increasing body size, but it remains unclear whether the increase is linear.

At the same time, a number of studies attempted to apply Lanchester's square law to intraspecific (Wilson et al. 2002; Plowes and Adams 2005; Batchelor et al. 2012) or interspecific (McGlynn 2000; Shelley et al. 2004) interactions among nonhuman animals. Although some of these analyses accounted for the fact that individual fighting abilities may differ between the opposing sides (Plowes and Adams 2005; Batchelor et al. 2012), others explicitly or implicitly assumed their equality (Wilson et al. 2002; Shelley et al. 2004). Such an assumption may be realistic for intraspecific combat, such as the chimpanzee intergroup contests analyzed by Wilson et al. (2002), but it is unlikely to hold for interspecific competition. In particular, Shelley et al. (2004) used linear group size (m, n) as the only predictor in their logistic regression analysis, which therefore amounted to a test not of the square law, but rather of a special case of the linear law, where $\alpha_m = \alpha_n$.

We aimed to investigate the validity of both Lanchester's laws while taking into account the different fighting abilities of the conflicting sides. First, we tested whether individual fighting ability was a linear function of body mass in accordance with the hypothesis implicitly formulated by McGlynn (2000) and Shelley et al. (2004). Under the assumption that dominance scales linearly with physical strength, this hypothesis contradicts the two-thirds power law which relates strength to the cross-sectional area of muscle ($F \propto m^{2/3}$) (Jaric 2002; Jaric et al. 2005; Folland et al. 2008). However, recent research suggests that at the whole-body level, force output scales linearly with mass rather than with the two-thirds power of mass in swimming, flying, and running animals (Marden and Allen 2002). It has been suggested that this reflects the fact that whole-limb force scales allometrically with muscle force in such a manner as to offset the allometric scaling of muscle force to muscle mass (Marden and Allen 2002). Because both hypotheses remain plausible, we explore the effects of using either of the 2 scalings in our test of Lanchester's laws.

To the best of our knowledge, Lanchester's laws have not been used to explain interspecific dominance relationships in marine ecosystems. A large body of ecological literature suggests that interspecific dominance hierarchies of herbivorous fish are established at the individual level by direct antagonistic encounters (Low 1971; Muñoz and Motta 2000). It has been assumed that the outcome of such confrontations is largely dependent on size (Robertson 1996, 1998; Munday et al. 2001) since larger body sizes allow fish species to gain access to territory, spawning, and food (Fausch 1998; Aas et al. 2010). Alternatively, studies have noted the role of group size in establishing dominance (Foster 1985). Despite the importance attributed to these factors, few studies have tested the dynamics between them that ultimately determine competitive outcomes.

Thus, we asked whether existing laws with already determined biological implications can explain interspecific behavior in coral reef fish. If either of Lanchester's laws holds, we will have evidence for a simple mathematical model describing interspecific interactions in marine habitats. Such a model would allow the prediction of competitive outcomes, thus becoming a valuable tool for modeling reef community structure, and this knowledge may facilitate ecosystem restoration and management.

MATERIAL AND METHODS

Data collection

Between 20 January and 5 February 2018, we observed interactions between 23 fish species (Table 1) within an approximately 150 m long stretch along the transition between the fringing reef and deeper waters at Maharepa, Mo'orea, French Polynesia (17°29′ S, 149°49′ W). This area contained both juvenile and adult fish. However, for species with age-based polychromatic differences (bullethead parrotfish *Chlorurus sordidus* and dark-capped parrotfish *Scarus oviceps*), we only focused on individuals that had reached their terminal adult phase, allowing for accurate identification. Juvenile parrotfish were treated as a separate ecospecies due to their physical similarity and tendency to forage in multispecies schools (Crook 1999). We documented interspecific displacements between both individuals and groups. A group was defined as an assemblage of conspecifics moving in a cohesive manner before and after a displacement. A displacement was defined as any interaction in which the arrival of an individual or group of 1 species within half a meter of an individual or group of another species caused one of the opponents to move away from the other. Our definition thus covers both displacements of previously present fish by a newly arrived competitor, and displacements of intruders by fish already present at the site of the interaction.

Twice a day, in the morning (7:30–11:00) and in the afternoon (13:30–15:30), 3 observers snorkeled independently along the fringing reef to observe displacements. For each interaction, we noted the time, the initiator (species A), the recipient (species B), group size of A, group size of B, and the winner.

Table 1

Body lengths and masses of the fish species observed at Maharepa, Mo'orea

Common name	Scientific name	Median body length (cm)	Estimated body mass (g)
Juvenile parrotfish	—	7	7
Lemonpeel angelfish	*Centropyge flavissima*	6	7
Bird wrasse	*Gomphosus varius*	9	9
Dusky angelfish	*Centropyge bispinosa*	7	11
Speckled butterflyfish	*Chaetodon citrinellus*	8	13
Sixbar wrasse	*Thalassoma hardwicke*	11	23
Oval butterflyfish	*Chaetodon lunulatus*	10	24
Scissortail sergeant	*Abudefduf sexfasciatus*	9.5	25
Longnose butterflyfish	*Forcipiger flavissimus*	11	39
Dusky farmerfish	*Stegastes nigricans*	10	39
Whitebar gregory	*Stegastes albifasciatus*	12	67
Brown tang	*Zebrasoma scopas*	14	78
Threadfin butterflyfish	*Chaetodon auriga*	15	85
Threeband pennantfish	*Heniochus chrysostomus*	14	88
Orange-lined triggerfish	*Balistapus undulatus*	18	109
Raccoon butterflyfish	*Chaetodon lunula*	16	110
Regal angelfish	*Pygoplites diacanthus*	17	128
Pacific butterflyfish	*Chaetodon ulietensis*	20	170
Moorish idol	*Zanclus cornutus*	16	171
Guineafowl puffer	*Arothron meleagris*	22.5	293
Dark-capped parrotfish	*Scarus oviceps*	25	312
Bullethead parrotfish	*Chlorurus sordidus*	25	339
Spotted porcupinefish	*Diodon hystrix*	35	1266

To estimate the sizes of the focal fish species, we first practised taking measurements by estimating the width of different coral structures and projections. Across observers, the mean absolute error was 2.17 cm (SD = 2.01 cm); paired *t*-tests were used to verify that no observer produced estimates that were significantly different from the true values ($n = 10$, all $P > 0.05$). We estimated 388 fish length measurements (per-species mean = 16.2, SD = 11.5). We tested for consistency of the medians of these values with maximum-attained sizes reported in the literature (Randall 2005) and found a strong correlation between the 2 ($r_p = 0.839$, $P < 0.001$). Furthermore, we used the median lengths to calculate body mass based on the allometric scaling factors reported by Brooks (2011); these were not available for our mixed category of "juvenile parrotfish." However, since parrotfish exhibit nearly isometric growth (El-Sayed Ali et al. 2011), we calculated the mass conversion factors for juveniles by averaging the values reported for bullethead and dark-capped parrotfish.

To supplement our live observations, we deployed video cameras to capture interspecific interactions. We set up six Crosstour CT7000 underwater cameras (Shenzhen Long Tou Optics Co., Shenzhen, China) to record footage at 1920 × 1080 and 30 frames per second. The length of the footage was limited by battery life and averaged 67.5 min. Similar to our live observations, video recordings were made twice a day. We repeatedly deployed the cameras at 6 nonadjacent locations spaced along 84 m of the fringing reef. The cameras were secured to a 30.5- × 61-cm wire mesh stabilized by a dive weight and rebar pole. Cameras were placed along the benthos ca. 2-m deep. To attract fish, *Padina boryana*, a highly palatable macroalgal species (Keeley et al. 2015), was collected from outside the Gump Marine Laboratory (17°29′32″ S, 149°49′39″ W) and fastened with zip ties to the other end of the mesh prior to deployment. After the completion of each recording, and on days when no cameras were deployed, we provided fresh bait to further encourage interactions at the study sites.

We collected a total of 97.9 h of footage recorded over 9 days, but the number of fish in our videos increased as fish became habituated to the cameras. Therefore, we focused on scoring the videos from the last 4 days. These videos were scored identically to the live observations. After scoring 18.2 h of recordings for a total of 206 observations, we plotted the number of unique species-pair interactions against the cumulative number of observations (Supplementary Figure S4). Since the curve began to flatten out, we scored no further footage.

We found similar levels of completeness and linearity as well as a significant correlation between the dominance hierarchies inferred from the data scored live and on video (Supplementary Tables S1 and S2; see also Supplementary Figures S1 and S2, Supplementary Tables S3 and S4), so we combined the 2 datasets and excluded all interactions involving unidentifiable species as well as 3 displacements involving blue-spotted cornetfish (*Fistularia commersonii*), a piscivorous species (Kalogirou et al. 2007; Takeuchi 2009) that was presumably more likely to participate in predatory rather than competitive interactions with other fish.

Estimating individual fighting ability

To tease apart individual fighting ability from group size effects, we subsampled our dataset to include only one-on-one interactions and discarded the composite category of juvenile parrotfish to facilitate controlling for phylogenetic nonindependence. In total, 389 out of 485 data points were retained. We created a taxon-by-taxon matrix with columns representing wins and identically ordered rows representing losses. The completeness of the matrix was calculated as the ratio of the number of nonzero entries to the total number of nondiagonal entries and equaled 34.6%. We quantified the extent to which the matrix conformed to a linear hierarchy using the modified Landau's h-index (de Vries 1995) that corrects for unknown interaction outcomes, as implemented in the R package *compete* (Curley 2016) and under the default setting of 10,000 randomizations. We found that the hierarchy was weakly ($h' = 0.28$) but significantly ($P < 0.01$) linear.

To quantify interspecific dominance, we used both the frequency of winning (defined as the ratio of the number of interactions a species won to the total number of interactions in which it participated; Wagnon et al. 1966) and the Clutton-Brock et al. index (CBI; Clutton-Brock et al. 1979, 1982) defined for each species i as

$$CBI_i = \frac{B + \sum b + 1}{L + \sum l + 1}, \tag{8}$$

where B is the number of opponents beaten by i, b is the number of species other than i that were in turn beaten by these opponents, L is the number of competitors i lost to, and l is the number of species other than i that these competitors lost to (notation after Clutton-Brock et al. 1979). CBI should be relatively robust to deviations from linearity, because it does not assume that dominance is transitive (Jameson et al. 1999). However, it does not consider asymmetry in repeated interactions (Gammell et al. 2003), which the frequency of winning explicitly accounts for.

We used phylogenetic generalized least squares (PGLS) as implemented in the R package *caper* (Orme et al. 2018) to control for autocorrelation due to phylogenetic relatedness when regressing dominance (as measured by CBI or winning frequency) on body mass (scaled either linearly or to the two-thirds power). We generated an ultrametric phylogeny for our 22 species by subsetting the time-calibrated tree of Rabosky et al. (2018) and transformed the corresponding variance–covariance matrix (VCV) by a maximum likelihood estimate of Pagel's λ (Pagel 1997, 1999). To assess the goodness-of-fit, we used the pseudo-R^2 statistic provided in *caper*, which fits an intercept-only model under the same VCV matrix and calculates the proportion of additional variance explained by the full model (Orme et al. 2018).

Testing Lanchester's laws

To distinguish between the linear and square laws, we subsampled our data to include only encounters involving different numbers of fish on each side (83 out of 485 observations). We predicted the outcome of each interaction under both models by multiplying the group size (linear law) or the square of the group size (square law) of either species by its body mass and selecting the competitor for which the product was greater. We also tested the fit of 2 additional models that only included the group size term (equivalent to setting $\alpha_m = \alpha_n$) or the individual fighting ability term (equivalent to the model of Shelley et al. (2004) in which $m = n$). We then compared the expected and observed outcomes, scoring successful predictions as "1" and unsuccessful ones as "0." We calculated the binomial probability of the proportion of successful predictions to determine whether it was higher than expected by chance. For the linear and square laws, the analyses were repeated with body mass raised to the two-thirds power. Note that because body mass scaling determines the relative weight of the body size and group size terms, it has no effect on the 2 alternative models that include only one of these variables.

RESULTS

Individual fighting ability

We found no significant relationship between body mass and either measure of dominance using the full 22-species dataset (Figure 1a and c). Using the two-thirds power of body mass as the predictor slightly increased the strength of the relationship with winning frequency (Figure 1d) but decreased it even further for CBI (Figure 1b). A visual examination of the results suggested that this result may have been driven by a single outlier (the spotted porcupinefish *Diodon hystrix*), whose body mass exceeded that of the second largest species nearly by a factor of 4 (Table 1). The exclusion of the spotted porcupinefish yielded a residual distribution that was both approximately normal and homoskedastic when visually examined following the recommendations of Mundry (2014). In all 4 cases, dropping the species increased the pseudo-R^2 values; however, the resulting relationships still failed to reach statistical significance. Both m and $m^{2/3}$ showed a marginally stronger relationship with the frequency of winning than with CBI, but this pattern reversed after outlier removal.

Lanchester's laws

The body size-only model and Lanchester's linear law successfully predicted displacement outcomes significantly more often than expected by chance (Table 2). The linear law performed better when individual fighting ability was approximated using isometrically ($\alpha \propto m$) rather than allometrically ($\alpha \propto m^{2/3}$) scaled body mass; however, the body size-only model marginally outperformed it even in the former case. In contrast, Lanchester's square law and the group size-only model performed no better or significantly worse than random chance (Table 2); the latter was the worst-fitting of all 4 models tested. The use of allometrically scaled body mass as a proxy for individual fighting ability further diminished the predictive success of the square law, consistently with its effect on the linear law. The linear law also consistently outperformed the square law in predictive power in subsampled analyses restricted to interactions between species from the same diet category (Supplementary Tables S5 and S6).

DISCUSSION

Individual fighting ability

To test the applicability of Lanchester's laws, we first had to estimate the individual fighting abilities α_m and α_n. We used body mass as a plausible approximation for fighting ability, following previous applications of Lanchester's laws to ecology (Franks and Partridge 1993; McGlynn 2000; Shelley et al. 2004) and a large body of literature on resource-holding potential (RHP) suggesting a close connection between the 2 (see Arnott and Elwood (2009) for a recent review). Based on a number of recent biomechanical studies (Marden and Allen 2002; Jaric et al. 2005; Folland et al. 2008), we used both isometric and allometric (two-thirds power) scalings of body mass to estimate α. From our results, we conclude that neither scaling explains a large amount of variance in the dominance measures used.

The weak relationship between body mass and dominance may reflect imprecisions in our body mass data, which were calculated from taxon-specific body lengths and conversion factors rather than

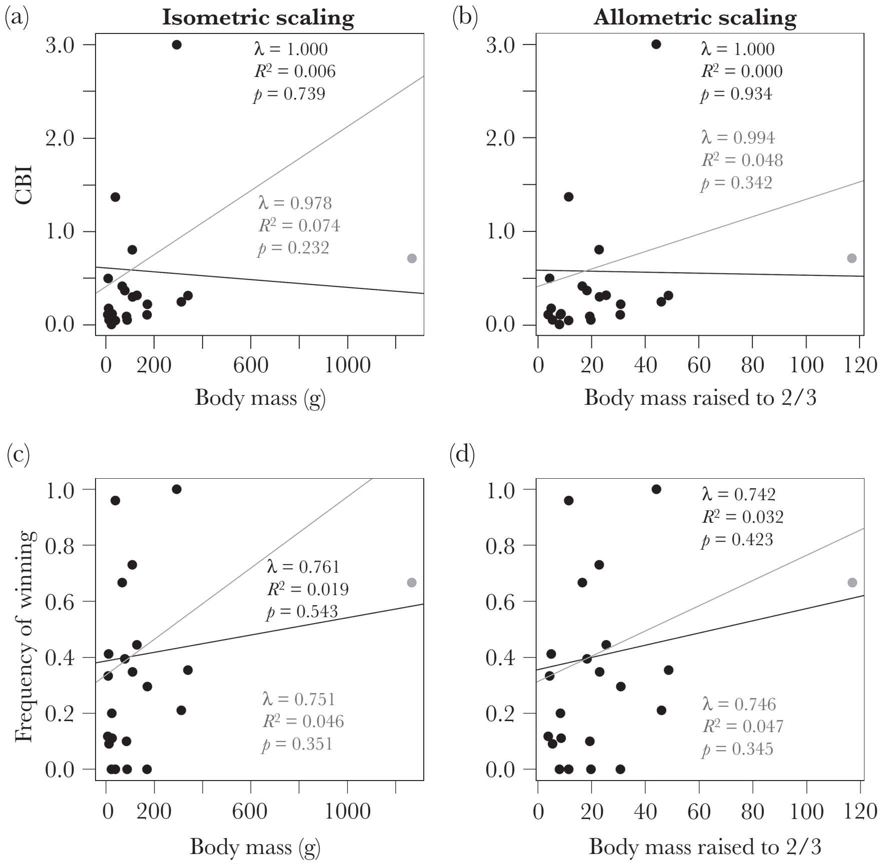

Figure 1

PGLS regressions of (a) isometrically scaled body mass m and CBI, (b) allometrically scaled body mass $m^{2/3}$ and CBI, (c) m and frequency of winning, and (d) $m^{2/3}$ and frequency of winning. Black, all species; gray, without spotted porcupinefish (marked in gray). Reported is the maximum likelihood estimate of Pagel's λ ranging from 0 (indicating no phylogenetic signal) to 1 (indicating trait evolution according to Brownian motion on the underlying phylogeny), the pseudo-R^2 measure of the goodness-of-fit, and the P value associated with the estimated slope. See Supplementary Figure S3 for the phylogenetically uncorrected regression analysis.

Table 2

Success of the 4 models in predicting displacement outcomes

Model	Success ratio		P_{null}	
Group size only	0.229		< 0.001	
Body size only	0.699		< 0.001	
	m	$m^{2/3}$	m	$m^{2/3}$
Linear law	0.663	0.566	0.001	0.042
Square law	0.494	0.361	0.087	0.004

P_{null} refers to the binomial probability of obtaining a given success ratio under the null hypothesis that predictive success and failure are equiprobable.

estimated or measured separately for each interaction. As a result, the value used might have been an underestimate or an overestimate for any given displacement. However, this problem is inherent to any attempt to assess interspecific dominance relationships. Aside from the practical difficulties involved, estimating body mass separately for each individual would analogously require determining each individual's CBI and winning frequency based on repeated interactions. This may be feasible in the terrestrial species for which these measures were first proposed, such as deer (Clutton-Brock et al. 1979) or cows (Wagnon et al. 1966), but not for a mixture of social and nonsocial species that are intermittently observed in an area which they are free to enter and leave. Even if it were possible to calculate dominance measures for each individual, it is unclear how the results could subsequently be grouped by taxon and used to construct an interspecific hierarchy.

Alternatively, the lack of a strong link between dominance and size can be seen as corroborating a number of recent studies which suggest that body size is of limited usefulness as a proxy for fighting ability (Barki et al. 1997; Neat et al. 1998; Stuart-Fox 2006; Arnott and Elwood 2009). In particular, aggressiveness is a better predictor of contest outcome than body size in a number of clades (Briffa et al. 2015), including fish (Carretero Sanches et al. 2012; Wilson et al. 2013). The propensity for aggression was also suggested to be the primary predictor of realized fighting ability in a recent application of Lanchester's laws to ants (Plowes and Adams 2005). Future studies of Lanchester's laws will benefit from better measures of individual strength.

Lanchester's laws

Somewhat surprisingly, our results suggest that the body size-only model, which ignores the number of individuals involved, best explains the outcomes of interspecific dominance interactions in a guild of reef fish. Of Lanchester's 2 models, only the linear law proved to be useful as a description of fish interspecific competition, consistent with the fact that it places greater importance on body size relative to group size than the square law.

The success of the body size-only model is unexpected given the importance often attributed to group size in shaping the outcomes of interspecific competitive interactions (Cooper 1991; Lehmann et al. 2017), including those among fish (Foster 1985; Ward et al. 2002). One possible explanation for this result is a lack of sufficient variation in the data: with a single exception, the dataset used to compare the 4 models only included encounters of a single fish of 1 species with multiple competitors of another species. Data from larger shoals may be needed to accurately evaluate the relative importance of group size and body size. Undue influence of outliers on the results also cannot be ruled out. Out of the 11 outcomes successfully predicted by the body-size only model but not by Lanchester's linear law, 8 involved dusky farmerfish (*Stegastes nigricans*), a territorial species (Karino 1995) that we observed to be particularly aggressive against intruders. Excluding dusky farmerfish from the dataset improves the fit of both the linear and (to a lesser extent) the square laws, with the former outperforming the body-size only model (Supplementary Table S7).

The universal lack of support for the square law across all tested scenarios (see also Supplementary Material) shows that interspecific displacements are not disproportionately influenced by group size. This might be due to the different nature of fish displacements compared with human combat. According to Lanchester (1916), group size doesn't scale with anything; on the contrary, overall fighting ability scales quadratically with group size. In the context of animal combat, this level of coordination is most likely to be present in social species (Plowes and Adams 2005). Although fish are social and capable of information transfer within shoals in many contexts such as predator inspection (Pitcher et al. 1986) and foraging (Day et al. 2001), they have not been shown to have complex coalitionary dynamics seen in primates and some other mammals (van Schaik et al. 2006) that can lead to coordinated attacks. Increasing group size alone does not necessarily imply an increase in coalitionary abilities.

Furthermore, the quadratic model may fit poorly to the fish displacement data because of its spatial implications. Lanchester (1916) applied his square law to modern warfare dominated by the use of long-range weapons. Unlike face-to-face fighting, firearms allow for more complex, long-ranged battles (Lanchester 1916). The small spatial scales on which our observed fish displacements occur (within 0.5 m) are more consistent with ancient human warfare where every attack is directly met. By de-emphasizing the concentration of force, this law is particularly applicable to close-quarters combat, which forms the bulk of interspecific antagonistic encounters among coral reef fish.

Generalizing Lanchester's laws may present a fruitful avenue for future research. Lanchestrian models with group sizes raised to continuously varying exponents have been independently proposed both in military (Bracken 1995) and ethological (Adams and Mesterton-Gibbons 2003) contexts. In both settings, values other than 1 (corresponding to the linear law) or 2 (corresponding to the square law) have been found to be optimal (Wiper et al. 2000; Plowes and Adams 2005; Johnson and MacKay 2008). Similarly, Cant (2012) pointed out that Lanchester's laws are models of infinite decisiveness, a feature that may not be realistic when conflict is risky for both sides. Allowing decisiveness to vary, as in the alternative tug-of-war model (Reeve et al. 1998), may be preferable in such cases.

Models predicting interspecific dominance hierarchies can provide insight into improving protocols for restoration ecology. Overfishing and habitat degradation threaten fish species worldwide (Turner et al. 1999; Jackson et al. 2001; Wilson et al. 2008). Fish hatcheries are used to raise the population size of the threatened and endangered species for later reintroduction to maintain populations; however, survival rates after release into the wild remain low (Brown and Day 2002). In attempts to increase these rates, programs have focused on individual characteristics such as size and fighting ability (Brown and Laland 2001; Vea Salvanes and Braithwaite 2006). However, to determine the probability of survival for social species, the dynamic relationship between an individual's competitive ability and the size of the group in which it interacts needs to be considered. To the extent that Lanchester's models of combat can be applied to this problem, Lanchester's linear law arguably provides a balanced trade-off between simplicity and predictive success.

SUPPLEMENTARY MATERIAL

Supplementary data are available at *Behavioral Ecology* online.

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Data accessibility: Analyses reported in this article can be reproduced using the data provided by Černý et al. (2018).

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