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Prevalence of Aggression as it Relates to Territory Size, Fish Density, and Neighbor Number in the Yellowtail Damselfish, *Stegastes arcifrons*

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Abstract: *Territoriality plays a key role in the survival and reproduction of many species. Damselfish (Family: Pomacentridae), reef-dwelling fish found in tropical locations, are territorial and competitively engage both intra- and inter-specific fish in order to protect their algal lawns. While damselfish territoriality has been examined as it relates to attack distance in con- and hetero-specifics, aggression in damselfish has not yet been related to fish density and proximity. The Galápagos yellowtail damselfish,* Stegastes arcifrons, *was selected for analysis of the factors that affect its behavioral aggression. Yellowtail damselfish individuals (n=31) were observed in the wild in 5-minute counts for aggressive interactions toward con- and hetero-specifics. The average location of the observed damselfish, including the locations of its nearby neighbors, was noted and dive markers were placed at these locations following the 5-minute count. Photographs of the average locations of the damselfish during the test, as shown by the dive markers, were taken and imaging software was used to determine damselfish density and an approximation of controlled territory through conversion into Voronoi diagrams. Aggression rates toward conspecific encounters, measured in aggressive attacks/minute, were positively correlated with damselfish density and inversely correlated with controlled territory size ($p < 0.001$ for both correlations, $R^2 = 0.52$ and 0.35 respectively). There were no significant correlations between aggression rates toward heterospecific encounters and any measured variables ($p > 0.05$ for all correlations). The number of nearby neighbors was also not significantly correlated with aggression ($p > 0.05$). Damselfish aggression is a direct function of both controlled area and conspecific density, but not of the number of nearby neighbors nor heterospecific individuals.*

Key words: *Damselfish, aggression, Galápagos, territory, algal, lawn, density, stegastes, arcifrons, yellowtail, competition, voronoi, territorial, reef, coral*

Introduction

The biogeography of the Galápagos Archipelago is structurally diverse, particularly due to its unique situation as the only tropical archipelago lying at the intersection of major warm- and cool-water current systems, namely the warm south-westerly flowing Panama Current, the cool north-westerly flowing Peru current, and the cold eastward-flowing subsurface equatorial (Cromwell) undercurrent (Houvenaghel, 1978; Edgar et al., 2004). With the distinct biogeographical differences found within the Galápagos come associated biota characteristic of various seas such as tropical (e.g. manta rays, reef sharks, corals and associated species), temperate (sea lions, kelp), and subantarctic (fur seals, penguins, albatross) (Edgar et al., 2004). Due to these significant variations in biogeography, many prior studies have been aimed at determining "regions" of similar biota, with major regionalization studies subdividing the Galápagos archipelago into either five (north, west, south, central, and central mixing) (Harris, 1969) or four (western, southern, central, and northern) (Wellington, 1975) regions. More recent data suggest a subcategorization of three major biogeographical areas, with two being further subdivided into two regions, each possessing communities characterized by a distinctive mix of species derived from Indo-Pacific, Panamic, Peruvian, and endemic source areas (Edgar et al., 2004). Of the species found to be highly correlated with a particular region includes the damselfish in the south-eastern region.

The damselfish genus *Stegastes,* within the Pomacentridae family, contains 7 species in the tropical eastern Pacific – *S. acapulcoensis, S. arcifrons, S. baldwini, S. flavilatus, S. leucorus, S. rectifraenum,* and *S. redemptus*. *Stegastes arcifrons,* the species selected for analysis in this study, is commonly known as the Galápagos damselfish due to its range which includes the Galápagos Archipelago and neighboring islands of Malpelo and Coco (Allen & Woods, 1980). *Stegastes arcifrons* is primarily a reef dwelling fish whose primarily source of nutrients comes from algal lawns which often abut coral colonies (Eaken, 1987). Damselfish display territoriality toward both con- and heterospecifics as a means of protecting their algal lawns, with many damselfish species maintaining nearly non-overlapping distributions with other damselfish species within specific reef zones while simultaneously excluding habitation by non-damselfish species (Ebersole, 1985). Territoriality is a behavioral trait that is prevalent throughout many different animal taxa. It has been demonstrated in animals ranging from marine iguanas, who compete to own and command a lek whose ownership is strongly correlated with breeding success (Partecke et al., 2002; Trillmich, 1983), to mockingbirds where dominant individuals directly sabotage mating and nesting interactions of nearby insubordinates (Curry, 1988). Territoriality can function to increase survival and reproduction and is thus frequently selected for (Hoffmann & Cacoyianni, 1989). Although territoriality isn't a viable behavioral strategy in all situations (an example being the decrease in territoriality efficacy as population size increases (Warner & Hoffman, 1980)), it is particularly prevalent in many damselfish species.

Territorial damselfish are commonly referred to as "farmers" as their role as small-bodied consumers and aggressive holders of benthic space allows for the maintenance of conspicuous algal lawns (Ceccarelli et al., 2005; Eurich et al., 2019). These interactions are mainly related to habitat selection: the rate of aggressive interactions between damselfish species is directly correlated with resource distribution (Robertson et al., 1981; Quadros et al., 2019) and is associated with the spatial and temporal variation in the branching corals among which they create their algal lawns (Chase et al., 2020). With greater resource availability come fewer instances of interspecific aggression, particularly when multiple species compete over an overlapping resource pool (Bay et al., 2001). Although the importance of habitat partitioning has been examined as it relates to damselfish aggression, to the author's knowledge behavioral studies into the rate of aggression as it correlates to neighbor proximity and density in damselfish have not been conducted. With an increase in neighbor number and damselfish density, the available resources are thus partitioned among a greater number of individuals, reducing availability for any specific individual.

The relationships between neighbor number, population density, and controlled territory size to aggression in the yellowtail damselfish, *Stegastes arcifrons,* were analyzed through this study. It was hypothesized that both the number of neighbors and damselfish density would positively correlate with aggression, while controlled territory size would negatively correlate with aggression. An increase in neighbor number and density would cause a concomitant increase in likelihood of interaction between any two damselfish, particularly in the setting of a more limited resource pool secondary to decreased availability of resources. Conversely, in the setting of larger territory sizes, damselfish are thus more distant from nearby conspecifics and are predicted to have fewer competitive interactions.

Methods

Yellowtail damselfish interactions were analyzed at multiple sites within the Galápagos archipelago between 17/04/17 and 28/04/17. The sampled locations included sites on and around Isabela Island (La Concha de Perla (n=5 sampled damselfish), La Calera (n=11), and the Loberia Grande (n=5)), as well as two locations near Floreana Island (Champion Islet (n=5) and Loberia at Floreana (n=5) (Table 1, Figure 1))). These sites were selected as they were similar with regards to species biodiversity and reef organization as determined by an experienced biologist familiar with the ecological makeup of Galápagos reefs, with each sampled location falling within the same biogeographical region (Harris, 1969; Edgar et al., 2004). Yellowtail damselfish were the only type of damselfish sampled in this study; thus, the use of the word damselfish is in reference to yellowtail damselfish unless otherwise noted.

Damselfish with territory size representative of their sampled location were selected for observation by a roving snorkeler. The distinction of a representative damselfish was made via several minute visual inspection of the territory for average size and substrate levels. Sites with minimal vertical relief were selected to better delimit territories. Yellowtail damselfish interactions were observed via a stationary snorkeler for 5-minute intervals, with aggressive interaction instances with conspecifics and other fish species recorded. An aggressive interaction, also called an attack, between a damselfish and another individual was defined as a chasing motion in which the observed damselfish engaged another fish by swimming at them, driving the other fish away from the guarded location. During the 5-minute interval, the center point of the damselfish's, and its surrounding neighbor's, territories were visually assessed. At the end of the 5-minute period, small fluorescent dive weights were placed at the approximated center points of each sampled fish (Figure 2a). A small 20cm scale-bar was placed near one of the fluorescent dive weights. A GoPro 5 Hero Black™ camera was used to take a picture directly above the center of the sampled damselfish's dive weight at a distance great enough to include

Table 1. Characteristics of Damselfish at Sampled Locations

	Champion	Concha de Perla	La Calera	Loberia at Floreana	Loberia Grande	Totals
Location	Floreana Island	Isabela Island	Isabela Island	Floreana Island	Isabela Island	
Latitude	1°14′21.14″S	0°57′43.97″S	0°57′52.71″S	1°16′54.20″S	0°57′42.19″S	
Longitude	90°23′7.00″W	90°57′26.56″W	90°57′22.26″W	90°29′31.88″W	90°55′41.63″W	
Type of Site	Exposed	Sheltered Lagoon	Sheltered Lagoon	Partially Sheltered	Sheltered Lagoon	
Sampled Damselfish	5	5	11	5	5	31
Damselfish Density (Fish/m^2)	0.12 (0.06)	0.36 (0.27)	0.54 (0.44)	0.71 (0.55)	4.10 (1.96)	1.08 (0.66)
Controlled Area (m^2)	1.06 (0.42)	0.60 (0.36)	0.47 (0.35)	0.46 (0.16)	0.18 (0.05)	0.55 (0.27)
Conspecific aggression (attacks/min)	0 (0)	0.40 (0.32)	0.78 (0.54)	0.70 (0.14)	0.96 (0.62)	0.60 (0.54)
Heterospecific aggression (attacks/min)	0.2 (0.14)	0.24 (0.22)	0.27 (0.13)	0.3 (0.14)	0.08 (0.18)	0.22 (0.17)
Number of Relevant Neighbors	3.8 (0.84)	4.6 (0.55)	4.0 (0.45)	3.5 (0.71)	4.2 (0.84)	4.1 (0.66)

All values given as "*mean (standard deviation)*"
Provides descriptive and quantitative data for the 5 sampled locations in the Galápagos archipelago

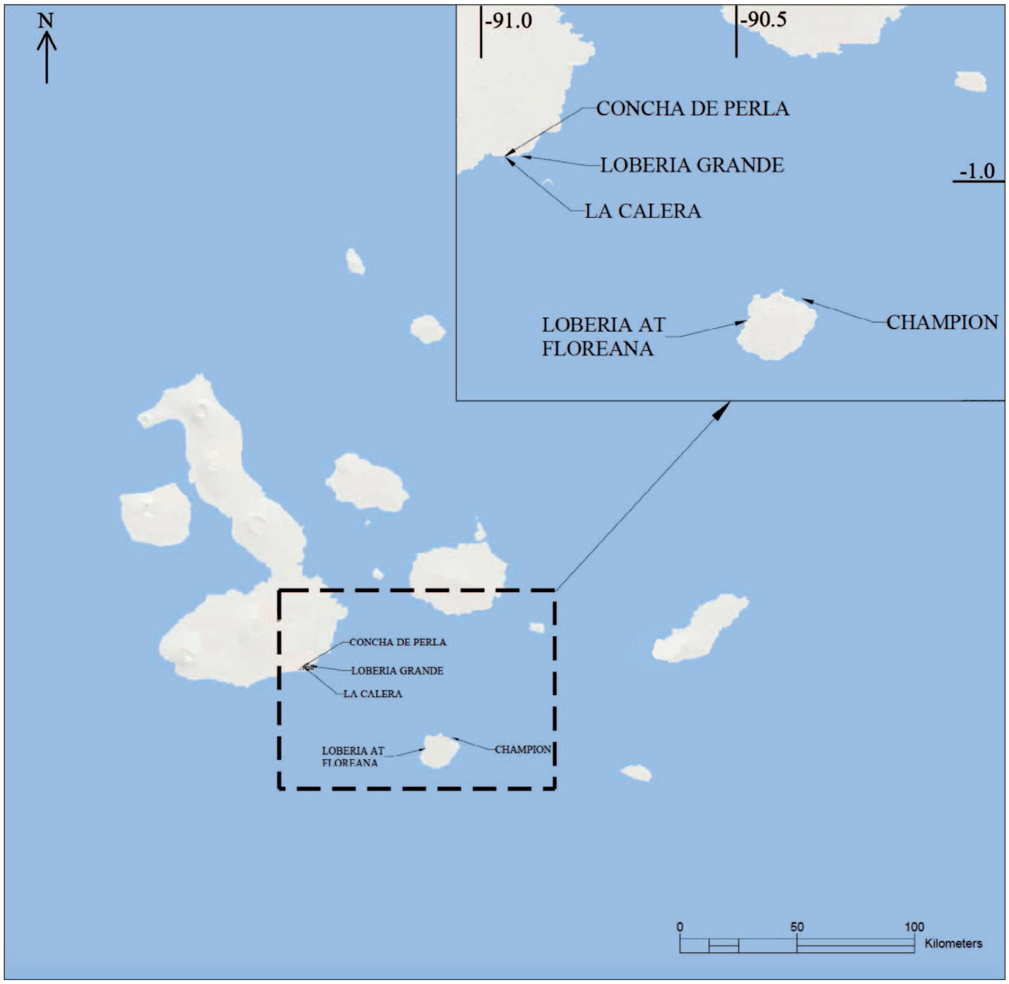
all of the neighbor's corresponding dive weights in the photograph. These photographs were overlaid onto a WebGL Voronoi diagram generator, created by Alex Beutel (found online at http://alexbeutel.com/webgl/voronoi.html), resulting in Voronoi diagrams based on the center points of the sampled and neighboring fish (Figure 2b).

Voronoi diagrams partition a planar image into regions based on their relative distances to target locations (in this case, the average damselfish locations during the 5-minute count) (Aurenhammer, 1991). The colored sections indicate area that is closest in linear distance to the particular dot within that area, giving an approximation of territory size. The regions of different colors thus approximate the controlled territory of each damselfish, with the caveat that only the territory of the central damselfish – the one whose competitive interactions have been recorded – is bounded as the neighboring damselfishes' respective neighbors were not included in the diagram. The black dots on the Voronoi projection refer to the location of the marked dive weights, which represent the determined center of the territory for all observed damselfish during the 5-minute observation. Sites with minimal vertical topography were selected to minimize territory size discrepancy after conversion to the 2D Voronoi view. Thus, the use of Voronoi diagrams in analysis of localized damselfish region can give rough approximations of controlled territories by calculating the 2D area that is closest in proximity to a particular individual (Figures 2a and 2b) (Okabe et al., 1994). The area within these boundaries is defined to be "controlled" by the central damselfish as it is closest in proximity to this damselfish, but the degree of control has not been determined experimentally. It is thus assumed for this analysis that territoriality occurs at each point equidistant to two damselfish territory center points.

The Voronoi diagrams were then analyzed with GIMP 2.8.20 software (The GIMP Team, 2017). Fuzzy selection, a tool used to place an outline overlaying an image where distinct colors intersect, of Voronoi boundaries gave precise pixel calculations of territorial area of the sampled damselfish. Measurement tools were used to determine pixel length of the scale bars within the photos, and conversions between scale bar length and pixel number gave the territorial area in standard units. The process of outlining the central damselfish's controlled territory on the Voronoi diagrams was repeated to determine total controlled area of the sampled damselfish, first in pixels and then in standard units. The pictures and corresponding Voronoi diagrams were used for determination of number of significant neighbors (i.e. individuals whose territories shared a common boundary with the sampled damselfish in the Voronoi projection).

Subsequent analysis of the photographs with the GIMP imaging software was performed to determine the population density of the yellowtail damselfish. Using methods derived from Clark & Evans (1954), the nearest distance to a conspecific of each fish captured in the photographs was determined through pixel-length measurements and subsequently converted into meters. The average of these nearest

Figure 1. Shows a map representation of the Galápagos archipelago with sampled locations indicated.



distance measurements was used in the calculation of population density for sampled damselfish as defined below:

$$\bar{\alpha} = {}^{1}\!/_{2\sqrt{\rho}}$$

where α is the distance in any specified units from a given individual to its nearest neighbor, and ρ is the density of the observed distribution expressed as the number of individuals per unit area.

The determination of significant differences between damselfish densities and territory size at the different locations was performed with ANOVA and post-hoc tukey HSD, and unpaired t-tests for normal data. Spearman's correlation was performed to assess significance of correlational data. Statistical tests were performed using a combination of Microsoft Excel, SOFA Statistics, and GraphPad Software. Select data were log-transformed to better ascertain significance. For all comparisons, significance was determined at an alpha of .05.

Results

Damselfish displayed different rates of aggressive behaviors towards conspecifics compared to heterospecifics. Damselfish attacked conspecifics at a significantly higher rate of 0.60 attacks/minute ($\pm$0.54) as compared to the heterospecific attack rate of 0.22 attacks/minute ($\pm$0.17) ($p < 0.001$, Table 1).

Average damselfish-controlled area varied between the sampled locations ($F = 6.049$, $df = 4$, $p = 0.001$). The average controlled area was significantly smaller at the Loberia Grande versus the Champion Islet ($p < 0.01$, 95%, $Q = 7.06$, Table 1). There was also a significant difference in average territory size between the La Calera and the Champion Islet sites ($p = 0.019$, 95%, $Q = 4.74$, Table 1), and between the Champion Islet and Loberia at Floreana sites ($p = 0.016$, $Q = 4.85$). No other site pairs differed significantly in territory size.

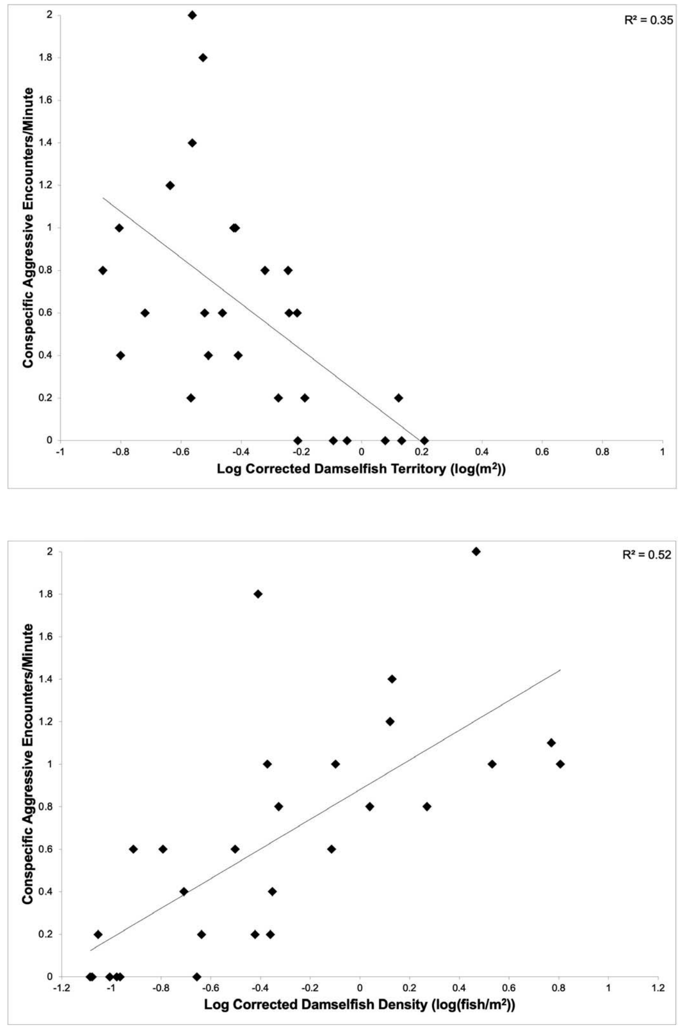
Damselfish density was statistically different between among sampled locations ($F = 20.254$, $df = 4$, $p < 0.0001$,

Figure 2a. Figure 2b. An example of a selected analyzed photographs from sample data (Fish #11, La Calera) and its Voronoi projection. Dive weights with orange markers were placed at the location of observed damselfish (Fig 1a), and Voronoi diagrams were overlaid on these images, with different colors indicating the area closest to each damselfish location (Fig 1b).

Table 1). The damselfish density at Loberia Grande was significantly greater than all other sites (Q = 10.08 for La Calera, 11.27 for Champion Islet, 9.61 for Loberia at Floreana, 10.6 for La Calera; $p < 0.0001$ for all comparisons).

The number of significant neighbors, other conspecific damselfish whose controlled area directly bordered that of the central sampled damselfish on their Voronoi projections, did not vary significantly among sampled sites ($F = 2.282$, $df = 4$, $p = 0.087$, Table 1), and showed no correlation with controlled area ($R^2 = 0.145$, $p = 0.14$) or damselfish aggression rate ($R^2 = 0.002$, $p = 0.89$).

Figure 3a. Figure 3b. Relationship between (A) aggression rate and damselfish-controlled area (m^3) ($R^2 = 0.35$, $p < 0.001$); (B) aggression rate and damselfish density in sampled locations ($R^2 = 0.52$, $p < .001$). Damselfish aggression was negatively correlated with controlled area and positively correlated with damselfish density.



The rate of damselfish aggression toward conspecific individuals, measured in aggressive encounters/minute, was inversely correlated with controlled territory ($R^2 = 0.35$, $p < 0.001$, Figure 3a). Similarly, the rate of damselfish aggression toward conspecifics was positively correlated with damselfish density ($R^2 = 0.52$, $p < 0.001$, Figure 3b). Damselfish, on average, engaged in more frequent displays of aggression in environments where they controlled a smaller territory, as well as where the overall damselfish density was greater. Conversely, damselfish aggression toward heterospecific individuals had no correlation with either damselfish territory size or density ($R^2 < 0.001$, $p > 0.05$ and $R^2 = 0.15$, $p > 0.05$ respectively).

Discussion

Both damselfish density and territory size showed significant correlations with instances of aggression toward other damselfish individuals, but no significant correlation was shown between aggression toward heterospecifics and territory size or density. Conspecific aggression was shown to scale logarithmically as the number of aggressive instances may be limited at extremes by energy expenditure and time allocation toward other activities such as breeding and reproduction (Viera, Viblanc, Filippi-Codaccioni, Cote, & Groscolas, 2011), with limitations on habitable space and substrate serving as primary motivators of intraspecific competition (Smith and Tyler, 1972; Robertson et al., 1981). Aggression toward heterospecifics was slightly, but not significantly, negatively correlated with damselfish density. Although this relationship was not significant, due to its similarity to density dependent aggression toward conspecifics, it is possible that significance could be realized through an increase in sample size. The decrease in aggression toward heterospecifics as damselfish population density increased is potentially due to non-damselfish species maintaining a farther distance away from damselfish territories with greater damselfish density. Given that damselfish are territorial and will attack many fish that come near their territories (Myrberg, 1972), the non-damselfish species would have a large incentive to avoid close contact with damselfish-dense areas. As spatial proximity was shown to be a factor affecting the rate of aggressive encounters between damselfish (Figure 3), this potential decrease in proximity between heterospecifics and damselfish in high-density areas would explain this slight correlation, though previous literature suggests it is not territory size but structural complexity of the reef that influences competitive interactions between and among reef species (Quadros et al., 2019). Habitat structural complexity and average distance between heterospecifics and damselfish and were not determined in this study.

Although it was initially assumed that number of neighbors sharing territory boundaries significantly correlate with aggression, there was no determined significance of this metric. The "dear enemy" phenomenon of less aggression toward neighbors than to strangers has been shown in many territorial animals (Temeles, 1994); it is thus possible that the number of immediate neighbors might not influence aggression in damselfish as much as transient damselfish passing by, explaining the lack of correlation between neighbor number and aggression. Additionally, an increasing number of relevant neighbors does not imply a decreased controlled territory size for any individual damselfish, and as the prime motivator for damselfish aggression is resource control, increasing neighbor number in the context of no significant change in controlled territory size is unlikely to effect a greater competitive response (Myrberg, 1972).

Of the three factors hypothesized to influence instances of aggression in the yellowtail damselfish, only two (damselfish density and territory size) were shown to correlate significantly, supporting the hypothesis that these factors are associated with increased frequency of aggression. Significant correlations were limited to aggression toward conspecifics; there were no sampled factors that showed significant correlation with aggression toward heterospecifics. It is likely that a lack of correlation between heterospecific aggression and any sampled variable was due to the less structured nature of heterospecific interactions as compared to conspecifics (i.e. heterospecific interactions depend on which fish happens to be swimming by rather than a fairly ordered population of the same damselfish species). Future studies into the potential factors affecting damselfish aggression toward heterospecifics should be conducted to better understand these interactions.

Conclusion

The Galápagos yellowtail damselfish, *Stegastes arcifrons*, engages in aggressive attacks towards conspecifics and heterospecifics as a means of protecting algal lawns. These aggressive attacks occur more frequently toward conspecifics in locations of high damselfish density and decreased territory size. The number of significant neighbors was not correlated with changes in the frequency of aggression. While no correlation was discovered between the number of hetero-specific species and damselfish aggression, the variety and number of non-damselfish individuals with which a sampled damselfish interacts is broad, making determination of significance difficult. Future studies aimed at addressing the interactions between damselfish and heterospecifics may prove fruitful at ascertaining such a relationship.

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