A. TITLE PAGE

Title: A test of the socioecological model in female Asian elephants: the effects of food abundance, food distribution, and competitor density on within-clan and between-clan contests

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Abstract

Socioecological theory, which attributes variation in social organization in female-bonded species to differences in within- and between-group feeding competition shaped by food distribution, remains largely unexplored in non-primate species. In the first such attempt on a non-primate mammal, we studied the patterns of agonistic contests within- and between-clans (the most inclusive social unit) of female Asian elephants with respect to food distribution, food abundance, and competitor density effects of group size and clan density. We directly quantified the distribution of grass biomass in different stretches of a grassland habitat around the Kabini backwaters, as well as the adjacent forest habitat, in Nagarahole National Park, southern India. We also quantified agonistic interactions among adult females in the grassland habitat to obtain rates of individual-level within-clan and between-clan agonism, and clan-level between-clan encounters. The occurrence of more frequent between-clan encounters in contrast to what was known from forest habitats, and stronger individual-level between-clan agonism than within-clan agonism was consistent with the grassland being a food-rich habitat patch as compared to the adjacent forest, as expected from socioecological theory. Within-clan agonism was not influenced by grass abundance or distribution within the grassland habitat, in contradiction to classic socioecological predictions, but interestingly increased with female group size until a group size of five, suggesting that the opposing forces of within-group and between-group competition may govern group size, as large group size is advantageous in this strong between-clan contest regime. The rate of (clan-level) between-clan agonistic encounters was positively explained by the number of clans. Although the rate of between-clan encounters was not related to grass biomass in focal zones, the duration of such encounters was positively related to grass biomass at the site of contest. We discuss contest competition in female elephant societies in

the context of socioecological theory.

Keywords: Socioecological theory, group size, feeding competition, within-group and between-group contest, agonism, food abundance and distribution, competitor density, fission-fusion, Asian elephants, Kabini Elephant Project, Nagarahole National Park.

Introduction

Socioecological theory offers a framework to explain variation in animal societies based on resource-risk distributions (Crook and Gartlan 1966, Alexander 1974, Terborgh and Janson 1986, Clutton-Brock 1989, Emlen 1995). The ecological model of female social relationships (EMFSR), which is part of the larger socioecological framework, proposes that feeding competition is a pivotal variable that shapes social organisation and structure in female-bonded groups (Wrangham 1980, van Schaik 1989, Isbell 1991, Sterck *et al.* 1997). Food characteristics, such as distribution, abundance, and quality, are expected to shape feeding competition regime. Within groups, scramble or exploitative competition is expected to predominate when limited food is dispersed and cannot be usurped by individuals, whereas strong contest or interference competition is expected when high quality food is present in usurpable clumps or patches (Janson 1985, van Schaik 1989, Isbell 1991). Between groups, contest competition is expected when food patches are large and can be usurped by groups (Wrangham 1980, Isbell 1991). Potentially strong and simultaneous between-group and within-group contest are expected to result in within-group contest being ameliorated via greater tolerance shown by dominant members of the group towards subordinates, since larger group sizes are likely to be advantageous during between-group contests (see Sterck *et al.* 1997, Isbell and Young 2002).

The role of food characteristics in shaping competition regimes and social relationships has been studied and discussed many times (for example, Janson 1985, Chapman *et al.* 1995, Koenig *et al.* 1998, Pruetz and Isbell 2000, Korstjens *et al.* 2002, see also Koenig 2002, Snaith and Chapman 2007). Based on mixed empirical findings, it has sometimes been suggested that other factors such as predation (Alexander 1974, van Schaik 1989), infanticide

(van Schaik 1996, Steenbeek and van Schaik 2001), or phylogenetic constraints (di Fiore and Rendall 1994, see Thierry 2013) may be as or more important than food characteristics in shaping female social organisation (see also Thierry 2008, Lawler 2011). Others (for example, Koenig and Borries 2009, Koenig *et al.* 2013) have defended the EMFSR, asserting that the model is based on solid reasoning. The interpretation of food abundance and distribution from indirect indicators such as diet type has been questioned instead (Snaith and Chapman 2007, Koenig *et al.* 2013, Wheeler *et al.* 2013), underlining the need for field-based quantification of food characteristics to test the ecological basis of contest competition. As contest competition may also be influenced by competitor density, group size and group spread may also be important to examine in the field (Wittig and Boesch 2003, Koenig and Borries 2006, Wheeler *et al.* 2013, see also van Schaik *et al.* 1983).

Despite the EMFSR not being conceptually restricted to specific taxa, it has been popular primarily among primatologists, and has rarely been examined in other mammals (but see, for example, Holekamp *et al.* 1996, Smith *et al.* 2008, Wittemyer *et al.* 2007, see also Caraco and Wolf 1975, Monaghan and Metcalfe 1985, Schmidt and Mech 1997). Thus, studies of the EMFSR on other taxa are desirable (Clutton-Brock and Janson 2012, see also Silk 2007). Even among primates, there has been a much larger body of work on the relationship between food distribution and within-group contest (for example, Janson 1985, Koenig *et al.* 1998, Pruetz and Isbell 2000, Korstjens *et al.* 2002, Koenig and Borries 2006, Chancellor and Isbell 2009, Hanya 2009) rather than on between-group contest (for example, Wilson *et al.* 2012, Brown 2013, Roth and Cords 2016, Pal *et al.* 2018). This is despite the fact that one of the principal disagreements between Wrangham's (1980) and van Schaik's (1989) early formulations of EMFSR was on the role of between-group contest in shaping female societies. Many studies of between-group contest have largely focused on territorial

behaviour or factors affecting outcomes of the contests or their consequences for group members (for example, Cheney 1987, Markham *et al.* 2012, Willems and van Schaik 2015, Roth and Cords 2016, Majolo *et al.* 2016, Mirville *et al.* 2018) rather than the effect of food distribution on between-group contests. Moreover, studies of within- and between-group contests have been carried out more often on frugivores (for example, Janson 1985, Vogel and Janson 2009, Chancellor and Isbell 2009, Hanya 2009) than on folivores (for example, Koenig *et al.* 1998, Harris 2006, Grueter *et al.* 2016, Teichroeb and Sicotte 2018), which were initially thought to face reduced feeding competition because of their seemingly low quality or continuously distributed and abundant diet (Wrangham 1980, van Schaik 1989, Isbell 1991). In the context of the above, we wanted to examine the relationship between food resources and rates of within- and between-group contests in a non-primate species, the Asian elephant (*Elephas maximus*), feeding primarily on grass, traditionally thought of as a low quality resource, in Nagarahole National Park and Tiger Reserve (Kabini population), southern India.

Asian elephants exhibit female-bonded groups (Sukumar 1989, Fernando and Lande 2000, de Silva *et al.* 2011), with the most inclusive social unit being the clan (Nandini *et al.* 2018). Females within clans show fission-fusion dynamics, in which clan-members are usually distributed across multiple groups, whose group compositions can change across hours (Nandini *et al.* 2017, 2018). A group is a "party" seen together in the field, with individuals usually within ~50 m of one another and showing coordinated movement. The home ranges of clans may overlap extensively (for example, Baskaran and Desai 1996, Fernando *et al.* 2008), a trait that is usually related to infrequent aggression during between-clan encounters since less exclusive ranges are associated with lower incentives of between-group aggression (see Cheney 1987, Willems and van Schaik 2015, see also Brown 2013, Pisor and Surbeck

2019). Male Asian elephants disperse away from their natal groups (Desai and Johnsingh 1995, Vidya and Sukumar 2005) and are largely solitary thereafter (Keerthipriya *et al.* 2018). Predation risk to adult female elephants in southern India is negligible, although calves may be occasionally taken by tigers. Female groups are not known to face any infanticide risks from males. Therefore, food characteristics, rather than predation or infanticide, are expected to shape group size and competition regimes in this species. Moreover, as female and male societies are largely separate, within- and between-group contest in this species do not typically involve the participation of adult males, unlike that found in some primates (for example, Cooper *et al.* 2004, Brown 2013, Pal *et al.* 2018). Thus, the Asian elephant is an excellent non-primate species in which to examine predictions of the EMFSR.

The Kabini elephant population, in which this study was carried out, has been monitored (Kabini Elephant Project) since 2009 and several hundred individuals identified and their clans known (see Methods). Contest competition is known to exist between adult females within clans as well as between clans in this population (Nandini 2016). Since elephants show fission-fusion societies, groups of females from the same or different clans can potentially interact with one another. However, we hardly ever found group-level agonistic interaction between groups from the same clan; therefore, between-group agonism in this paper refers to agonism between clans. The nature of dominance relationships has also been studied in another Asian elephant population (de Silva *et al.* 2017), but there has been no actual quantification of food resources or an attempt to relate them to contest competition in any elephant species. In this paper, we directly quantify food abundance and distribution in a small grassland habitat, and study their relationship with the frequency of agonistic interactions within and between clans. We also examine the effect of group size on such interactions. Proximal understanding of agonistic contest competition in Asian elephants can

help in assessing the socioecological model in a species that falls towards the egalitarian side (Nandini 2016, de Silva *et al*. 2017) of the egalitarian-despotic continuum.

We addressed the following specific questions.

1) How does grass abundance in the Kabini grassland compare with that in the neighbouring forest habitat, and what is its distribution across and within different areas (focal zones) in the grassland?

Since between-group contests are more frequent in the Kabini grassland (Nandini 2016) compared to the nearby forests in the Nilgiri Biosphere Reserve (Baskaran 1998), we wanted to find out whether the former was richer in resources, possibly explaining the occurrence of between-group contests. We thus expected greater grass biomass in the Kabini grassland than in the forest, which also has grass understorey. We did not expect much spatial variation in grass abundance at a local level (within focal zones – see Methods) in the grassland because the grass layer appears to be continuous (see photos in Supplement1). However, we expected a few focal zones in the grassland to have greater grass biomass than others as grass height seemed to vary based on preliminary visual assessment.

2) How do the rates and intensities of individual-level agonism among females compare within and between clans?

As mentioned in the Introduction, strong between-group contest is expected according to the EMFSR when there are large patches with abundant food, whereas contest among females within groups is expected to be more frequent when feeding sites are clumped at the local level (Wrangham 1980, Sterck *et al*. 1997, see Koenig 2002, Snaith and Chapman 2007). Therefore, we expected that if the grassland habitat were a food-rich habitat and if there were significant differences in grass abundance across focal zones, agonism among individual

females would be more frequent during between-clan encounters than within clans. This would not ensue merely because of the larger number of females present during between-clan encounters, but the rate of individual-level agonism (number of agonistic events per female per hour) during between-clan encounters would be greater than that within clans after controlling for the number of females. In this case, we also expected the intensity of agonistic interactions to be higher during between-clan than within-clan agonistic interactions. On the other hand, if there was little variation in grass abundance across zones and high local variability, we did not expect the rate of individual-level agonism to be different between and within clans (the presence of more than one clan in a feeding area would not increase the rate of individual-level agonism because females would not be expected to give up their feeding time to participate in between-clan agonistic interactions if the patches were not large enough to be usurped by clans).

3) Is the rate of within-clan agonism explained by variation in grass abundance, grass dispersion, and group size?

We wanted to examine whether the rate of (individual-level) within-clan agonistic interactions was explained by grass abundance and dispersion, and group size. From the classical prediction of EMFSR (for example, Koenig *et al.* 1998, Pruetz and Isbell 2000), we expected within-clan agonism to be more frequent when grass was more clumped at a small spatial scale. In accordance with simple models of feeding competition, we expected more frequent agonism where grass was scarce. We expected group size, which reflects local competitor density, to positively correlate to within-clan agonism (see Koenig and Borries 2006, Wheeler *et al.* 2013).

4) Is the rate of individual-level between-clan agonistic interactions explained by variation in grass abundance, grass dispersion, and group size?

Similar to the question above, we also wanted to examine whether the rate of individual-level between-clan agonistic interactions was explained by grass abundance and dispersion, and group size. We expected the rate of individual-level agonistic interactions between clans to be positively related to food abundance at the site of contest. Further, we expected the rate of individual-level agonistic interactions between clans to be higher when the competing clans were evenly matched in group size, a determinant of resource holding potential of groups (for example, Roth and Cords 2016), than when there were large differences in group sizes.

5) Are the rate of clan-level between-clan agonistic encounters and the duration of such encounters related to grass abundance/distribution and group size or the number of clans?

As with individual-level interactions, we wanted to examine how well the rate of between-clan agonism at the level of the entire groups participating (clan-level) could be explained by grass abundance and dispersion, and clan (group) density. Game theory explanations expect the nature of contests to depend on the resource value of the site contested and resource holding potential of the contestants (for example, Markham *et al*. 2012, *sensu* Smith and Parker 1976). Applying this to clan-level contests, we expected more frequent clan-level between-clan agonistic encounters in focal zones with more abundant grass since between-group contest is thought to be linked to food abundance (Koenig 2002). Further, we expected more frequent clan-level between-clan agonistic encounters in zones within which grass was heterogeneously distributed than in zones with dispersed grass (see Methods). Following from van Schaik's (1989) prediction of stronger between-group contest at high density, we also expected more frequent between-clan agonistic encounters when a larger number of clans was present in the zone. We expected the duration of such clan-level agonistic

encounters to be positively related to food abundance at the site of contest. We also expected that the duration would be higher when the competing clans were evenly matched in group size than when there were large differences in group sizes.

Methods

Study area

We carried out the study in Nagarahole National Park and Tiger Reserve (11.85304°-12.26089° N, 76.00075°-76.27996° E) in the Nilgiris-Eastern Ghats landscape, southern India. Nagarahole largely comprises deciduous forest with grass and other herbaceous and shrubby plants in the understorey, but an open grassland is formed by the receding backwaters of the Kabini reservoir (formed by the Beechanahalli Dam built on the River Kabini that flows between Nagarahole and Bandipur National Parks) during the dry season (Figure 1a). This grassland supports a high density of wild herbivores, including elephants. Hundreds of elephants that use the Kabini reservoir and its surrounding forests have been identified based on natural physical characteristics (see Vidya *et al.* 2014) and monitored since 2009 as part of the long-term Kabini Elephant Project in order to understand their ecology and behaviour. The grassland around the backwaters has a continuous layer of grass (see Supplement 1), which is the primary food for elephants there. Bamboo clumps around the backwaters that were previously used by elephants died out after the mass-flowering in 2011. Spatio-seasonal variation in the abundance of elephant food plants in the forested area of Nagarahole is described in Gautam *et al.* (2019).

Data collection

Sampling of grass abundance and distribution

Around the backwaters area, six grassland stretches, henceforth called focal zones (Figure 1b), were selected for sampling. Each focal zone allowed for clear visibility of a considerably large grassland area from either end, and could be demarcated from adjacent zones by either the abrupt narrowing of grassland strips along the river or by physical breaks such as small streams. Because of water lever fluctuations in the reservoir, the areas of focal zones varied across different months (Supplement 2). We sampled four periods of about 30 days (henceforth, referred to as months) during the dry seasons of 2015 and 2016. In each focal zone, we sampled 20 1m x 1m quadrats each month, almost always on a single day in the middle of each 30-day period. These 20 quadrats were distributed within each zone in 4 clusters (henceforth plot-clusters) of 5 quadrats each (see Figure 1c) in order to sample different areas within a zone and assess the variability of grass abundance at a local scale. While the centre of a plot-cluster was fixed across months, we laid the five constituent quadrats by walking random distances along a random direction (using randomly generated numbers) each month. Random sampling was chosen because grass appeared to be continuously spread and it was not possible to visually detect either the centre or the extent of patches, unlike in studies on primates where patches may be more clearly delineated (tree trunk and canopy spread, for example, Vogel and Janson 2011). We visually estimated the percentage grass cover (see Gautam *et al.* 2017), measured grass height, and harvested fresh biomass from each quadrat (see Supplement 1). We measured grass height in a quadrat as the average of the natural standing heights (i.e. without straightening the plant) of ten grass stems within that quadrat. We clipped all the grass above the ground level, separated them from herbs if they existed, and weighed the fresh harvested grass biomass in the field using a digital weighing balance.

For comparison of grass abundance between the grassland and the forest habitat, we used harvested grass biomass data from vegetation transects sampled previously (Gautam *et al.* 2017) from forests of Nagarahole National Park. The three major forest types (dry deciduous, moist deciduous and teak forests) were sampled proportionate to their land-cover. We collected data from the forests at the end of the wet season (November-December).

Sampling of focal zones to quantify within-clan and between-clan agonism

We carried out full-day observations on selected focal zones during the four sampling months each year to quantify elephant visits and agonistic interactions between elephants. We selected the focal zone to be sampled based on rotational sequence, and sampled each zone on three sampling days during each sampling month in 2015 and four such days in each sampling month in 2016. We additionally carried out opportunistic sampling on the remaining days when possible in order to maximize observations of agonistic behaviour. On each sampling day, the observer (HG) remained in the selected focal zone from approximately 6:30 AM to approximately 06:30 PM (based on permits) and recorded all elephant visits to the zone. We collected details on the time of arrival and departure of elephant groups, group size, group composition (counts of adults, sub-adults, juveniles, and calves, of each sex), and the identities of all the individuals based on natural physical characteristics (see Vidya *et al.* 2014), subsequently verified from photographs and videos. As mentioned above, a female group is a party or set of adult females (and other associated individuals) seen in the field that show coordinated movement and/or affiliative behaviour and are usually within ~50 m of one another (see Nandini *et al.* 2018). Female groups are usually subsets of clans, which are the most inclusive female social units, and within which associations are fluid, showing fission-fusion dynamics (Nandini *et al.* 2017, 2018).

Since the open grassland had complete visibility, we used focal group sampling (see Altmann 1974) to record agonistic interactions between adult females, defined as females that were at least 10 years old (see Nandini *et al.* 2018) at the mid-point of the sampling period, i.e., 1 October 2015. Adult females are, henceforth, referred to simply as females in this paper. Such agonistic interactions could occur between females within groups, and therefore, belonging to the same clan, or between members of different groups belonging to different clans. As mentioned above, we hardly ever saw group-level agonistic interaction between different groups belonging to the same clan. Therefore, our interest was in comparing within-clan and between-clan agonistic interactions. We recorded focal observations using a Sony HDR-XR100E video camera and noted down GPS locations and the predominant activity of the group (feeding, using water/puddles, or other activity). We focussed videos in such a way as to attempt recording all the females within a group. However, if the females were spread over a large area and recording of all females was not possible, we took down field notes on the females outside the video frame. This rarely happened during within-clan agonism.

For all focal group observations, we also noted down the nearest plot-cluster so that the relationship between grass abundance/distribution and agonism could be examined. We did not assign any plot-cluster to a focal group observation if the focal group was more than 100 m away from the centres of all plot-clusters.

Video scoring

We used the video recordings to score (in VLC media player) agonistic interactions between females. Agonistic interactions included aggressive behaviours such as displacement, supplant, pushing, shoving, trunk wrestling, hitting, kicking, chasing, charging, placing trunk

over opponent's head to dominate, and pulling tail, and submissive behaviours such as turning away and showing back/urinating/shaking head after advancing towards an opponent, submissively walking backwards towards the opponent, and avoidance. We also used supplemental field notes, but excluded any focal group observation from calculations of rates of agonism if we did not have a complete record of agonistic behaviours performed by all females. We also excluded focal videos if the elephants were disturbed and their activity disrupted.

We classified focal observations of individual-level agonistic interactions between females into two categories – within-clan and between-clan agonism. Between-clan interactions could be examined at the level of the individual females participating, as well as at the level of the entire groups present, which we refer to as clan-level interactions/encounters or outcomes. We recorded the time of individual interactions, and the identities of the initiator, recipient, winner, and loser in within-clan and between-clan agonistic interactions between females. In addition to these individual-level details, in the case of between-clan interactions, we also recorded the start and end time of clan-level between-clan encounters (see below), clan identities of the competing groups, and whether the group won or lost if there was a clear resolution at the level of the entire between-clan encounter. We noted a between-clan encounter as having begun if the individuals at the closest edges of two groups from different clans approached to within a distance equivalent to the spread of the larger of the two groups, or to within a distance of ~50 m (if their spread was smaller than ~50 m). We noted the encounter as having ended if one or both clans started walking away and the distance between them exceeded this threshold. We classified between-clan encounters as agonistic, if there was at least one agonistic interaction between females of the competing clans, or not. We scored the outcome of the entire between-clan agonistic encounter (clan-level outcome),

which could comprise multiple individual-level agonistic interactions between the females of the participating clans, as having a clear resolution if one of the two interacting groups (the winning clan) dominated and completely displaced the other group (losing clan) from the place of encounter by more than the maximum group spread of the larger of the two groups (or by more than ~50 m if their spread was much smaller).

Data analysis

1. How does grass abundance in the Kabini grassland compare with that in the neighbouring forest habitat, and what is its distribution across and within different areas (focal zones) in the grassland?

In order to test for differences in grass abundance between the grassland and forest habitats, we compared the harvested biomass from the plot-clusters (average of five 1 m x 1 m quadrats each) in the grassland habitat (N=95 and 96 plot-clusters in 2015 and 2016, respectively) with that from plots in forest habitat (N=40 plots, averages of three 1 m x 1 m quadrats per plot). Since the forest data was collected only once and in a previous year (end of wet season of 2013), we compared it separately with the grassland data from 2015 and 2016. We performed t-tests with unequal variances, since the two habitat types had unequal variances, in MS Excel. Along with these statistical tests, we also used previously published grass biomass from Bandipur National Park (Devidas 1995), to compare with our data. For this, we calculated the average grass biomass from the same months as in our sampling (February to June), and used Welch's test (Welch 1938, see Fagerland and Sandvik 2009) to compare the averages.

In order to examine the distribution of grass abundance in the grassland habitat, we used three measures of grass abundance – biomass, cover, and average height. We averaged values of

each grass abundance variable from the five 1 m x 1 m quadrats of each plot-cluster to obtain average abundances that we refer to as within-plot-cluster biomass/cover/height. We also calculated variability as the coefficient of variation (CV=standard deviation to mean ratio) based on the five quadrats of each plot-cluster to obtain within-plot-cluster CV in grass biomass, cover, and height. These values would indicate the local abundance and local variability within a plot-cluster, which would be relevant to within-clan feeding competition. For the four plot-clusters, in which data from a quadrat each was missing either due to rain or other logistical problems in the field, we assigned the average abundance value of the other quadrats to the missing cell.

We averaged grass abundances from all the four plot-clusters within each zone to obtain within-zone grass biomass/cover/height, which was taken as representative of the zone's average grass abundance. We also calculated the within-zone CV in grass biomass/cover/height across the four plot-clusters within a zone, as estimates of the variability within each zone. Within-zone abundance and variability were expected to influence between-clan contest, the former being a measure of average food abundance for the entire zone and the latter providing information on heterogeneity across plot-clusters, which could presumably be perceived by clans to contest for foraging patches.

We then used a mixed-effects General Linear Model (GLM) to test the effects of year (random factor), month (fixed factor), zone (fixed factor), and their two-way and three-way interactions on the dependent variable, which was the within-plot-cluster grass abundance (a separate GLM was carried out for within-plot-cluster biomass, cover, and height). As mentioned above, the five constituent quadrats of each plot cluster were chosen randomly each month; therefore, month was not a repeated-measure. Data were missing for one data

point (plot-cluster), and we used the mean of the other three plot-clusters for this point in order to obtain a balanced design.

2. How do the rates and intensities of individual-level agonism among females compare within and between clans?

Since we wanted to compare the rate of individual-level agonism within and between clans, we focused on the occurrence of agonistic contests and not their outcomes. We used the average rate of agonistic interactions between females (individual-level agonism), calculated from focal group observations, as a measure of contest competition (see Koenig *et al.* 2013). We only included focal observations in which the group's predominant activity was foraging, so that the rates of agonism primarily reflected interference during foraging, and consequently, loss of feeding time and opportunities (see Janson 1985). We considered an agonistic interaction between two females to be independent of another interaction between the same pair if the two interactions were at least 15 minutes apart. This was because we found that in more than 95% of the cases, the interval between an individual-level agonistic interaction and the subsequent interaction involving the same dyad was less than or up to 15 minutes, making this a meaningful cut-off for both within-clan and between-clan individual level agonism (Supplement 3). We classified interactions that occurred within 15 minutes of each other involving the same dyad as non-independent interactions. We excluded focal group observation videos if they were shorter than 15 minutes. Additionally, if the same group (same female composition) was recorded again for within-clan agonism after an interval, we included the subsequent video for scoring only if there was a gap of at least 15 minutes.

In order to calculate the rate of individual-level agonism during between-clan interactions, we used focal group observations of all between-clan encounters, whether they were agonistic or not. We used a 2.5-hour cut-off to define independence of focal group observations on between-clan encounters. This was because more than 95% of between-clan encounters at the level of the clans, for which exact start and end times were known, occurred for less than or up to 2.5 hours (Supplement 3). Subsequent encounters between the same two clans were considered non-independent at the clan-level and excluded from this analysis if they occurred within 2.5 hours of the first encounter.

We used only the independent individual-level interactions from each independent focal session (either within or between clans) to calculate the rates of individual-level agonism in two ways: rate of agonism per female per hour and dyadic rate of agonism (see Table 1 for formulae). While the rate of agonism per female per hour reflects contest or interference competition (see Wheeler *et al.* 2013, Koenig *et al.* 2013), the dyadic rate of agonism measures a female's interaction rate with every other competitor (Cowl and Shultz 2017). We additionally calculated the simple ratio of non-independent interactions to independent interactions (NI/I ratio) during each independent focal group observation with at least one individual-level agonistic event, as a measure of the intensity of individual-level agonism during within-clan and between-clan interactions.

We used linear mixed-effects models to investigate the effect of type of agonism (between-clan/within-clan, fixed effect) on rates of individual-level agonism. Since our agonism data were from multiple clans, we included clan identity as a random effect. However, there were not enough focal observations of both between-clan and within-clan agonism for many clans. Therefore, we used data from the five common clans (minimum of eight focal observations

each of within- and between-clan agonism) for this analysis. In addition to this, we also plotted the rates of individual-level within-clan and between-clan agonism, including other clans as well. The mixed-effects model was used separately for the per female rate and dyadic rate of agonism. We also tested for the difference between within-clan and between-clan agonism in the intensity of agonism (NI/I ratio), but we used a fixed-effects model since clan did not explain any variation in NI/I ratio.

In order to examine if the rate of individual-level agonism within and between clans remained significant after controlling for the number of female competitors (group size for within-clan and sum of group sizes for between-clan encounters), we used a homogeneity-of-slopes test and regressed the rate of individual-level agonism on the number of female competitors, with type of encounter (within-clan and between-clan as two levels) as a categorical variable. Since clan identity did not explain much variance in the above analyses (see Results), and since many clan combinations had small sample sizes, clan identity was not included as a random effect.

3. Is the rate of within-clan agonism explained by variation in grass abundance, grass dispersion, and group size?

In order to examine what explained within-clan agonism, we included only those independent focal group observations for which we also had data on grass abundance and variability, i.e., observations of groups that were within 100m of the centre of one of the four plot-clusters that had been sampled for grass abundance. We used linear mixed-effects models (*lmer* function in *lme4* package in R, Bates *et al*. 2011, R Core Team 2018) to test how the within-clan rate of individual-level agonism (calculated for each focal group observation as described in the section above) was influenced by within-plot-cluster biomass, cover, and

height, within-plot-cluster CV in biomass, cover, and height (from the nearest plot-cluster), female group size, month, and zone (all fixed effects), and clan identity and year (all random effects). We selected the best-subset model based on AICc (*dredge* function in *MuMIN* package, Barton and Barton 2012). In case the model failed to converge or if there was singularity due to random effect(s) explaining negligible variance (<0.001), we excluded those random effects and tested fixed effects models using *lm* function of *lme4* package and ran the best-subset selection again using *dredge*. The analyses were carried out separately on the (individual-level within-clan) rate of agonism per female and the dyadic rate of agonism.

We also examined the effect of female group size on the within-clan rate of agonism per female in more detail and performed a piece-wise regression analysis on the dataset since there visually appeared to be a non-linear relationship.

4. Is the rate of individual-level between-clan agonistic interactions explained by variation in grass abundance, grass dispersion, and group size?

We used the same independent focal observations of between-clan encounters during which the groups' predominant activity was foraging, and which occurred within 100 m of the centre of one of the four plot-clusters that had been sampled for grass abundance. Since the random effect of year explained negligible variance and resulted in singularity in mixed-effects models, we used linear fixed-effects models (*lm* function in *lme4* package in R) to look at the effects of month, zone, within-plot-cluster grass abundance (biomass, cover, and height), within-zone grass abundance, within-zone grass variability (CV), and sum of female group sizes of the two groups (all fixed effects). We chose the best-subset model based on AICc as described in the previous section.

5. Are the rate of clan-level between-clan agonistic encounters and the duration of such encounters related to grass abundance/distribution and group size or the number of clans?

We divided each sampling day in a focal zone into four 2.5-hour intervals (08:30-11:00, 11:00-13:30, 13:30-16:00, 16:00-18:30) and counted the number of clans present and number of between-clan agonistic encounters (at the clan-level) occurring within each 2.5-hour interval. The temporal resolution (2.5 hours) is meaningful because, as mentioned above, more than 95% of between-clan agonistic encounters lasted less than or up to 2.5 hours (Supplement 3). For each 2.5 hour interval with two or more clans (intervals with 0 or 1 clans in the focal zone were excluded because there was no potential for between-clan contest in such cases), we calculated the rate of between-clan agonistic encounters per clan using the formula given in Table 1, wherein the count of clans reflects the number of potential competing parties at the clan level. We explored the effects of month, zone, within-zone grass abundance (biomass, cover, and height) and within-zone variability (CV) in grass abundance, the number of clans present, area of the focal zone (all fixed effects), and year (random effect) using linear mixed-effects models (as described in a section above) and selected the best subsets based on AICc, to explain the rate of between-clan agonistic encounters. The number of clans would reflect the local density of competing parties during between-clan contest and area of the focal zone would take into account any confounding effect of a greater number of clans being found in larger focal zones. It turned out that the random effect of year explained negligible variance (<0.001); therefore, we excluded it and explored only fixed effects models using *lm* function of *lme4*package and ran the best-subset selection again using *dredge*.

To analyse the durations of clan-level between-clan agonistic encounters, we excluded the clan-level encounters for which the complete durations were not known, for example those

that began at the end of the day or extended beyond the permitted sampling time or those for which the exact time was not known. We then used fixed-effects models and subsequently selected best-subsets (based on AICc) to find out which variables among within-plot-cluster grass abundance, within-zone grass abundance and variability (CV) variables, sum of female group sizes (from the two competing clans), and difference in female group sizes of the two groups could explain the duration of agonistic between-clan encounters. Including the sum of group size in the analysis would reveal if the presence of a larger number of females prolonged the duration of between-clan encounters, whereas including the difference in group sizes in the analysis would help in testing whether between-clan encounters last longer when competing groups are of similar strength. We did not use month and zone because the sample sizes of some of the levels within them was very small. We found that two grass abundance variables in the best model showed Wald statistic (t) in opposite directions (see Results). Therefore, we partitioned the variances using the ANOVA tables obtained from *anova()* function and obtained η^2 to infer which variable had a stronger effect.

Software

All ANOVAs on grass abundance were carried out using Statistica 7.0 (StatSoft Inc. 2004) but the appropriate F test calculations were done based on Neter *et al*. (1990, Chapter 27, pgs. 1010-1029), and η^2 was calculated to measure effect size for each term ($SS_{effect}/SS_{corrected\ total}$, see Fritz *et al*. 2012). For comparing the means of two groups, we used Cohen's d (d=difference in means/pooled standard deviation, Cohen 1988) as the effect size. For mixed-effects models of rates of agonism, multiple R^2 was obtained from the *lm* output, while for the mixed models we used *r.squaredGLMM* function of R package *MuMIN*. The latter provides R^2 (marginal), which includes only the fixed effects, and R^2(conditional), which also includes

the variance explained by random effects (Nakagawa and Schielzeth 2013). All plots were made in Statistica 7.0 (StatSoft Inc. 2004).

Results

1. How does grass abundance in the Kabini grassland compare with that in the neighbouring forest habitat, and what is its distribution across and within different areas (focal zones) in the grassland?

1a. *Difference in grass abundance between grassland and forest habitat:* Grass biomass in the grassland habitat from both 2015 (t=14.187, P (one-tailed) <0.001) and 2016 (t=15.300, P (one-tailed) <0.001) were higher than that in the Nagarahole forest habitat (Figure 2a). The average grass biomass in the grassland habitat (2015: mean=704.78, 95% CI: 646.04—763.51 g/m^2, N=95 plot-clusters; 2016: mean=583.46, 95% CI: 546.58—620.34 g/m^2, N=96 plot-clusters), despite being sampled during the dry season, was about or over three times greater than that in the forest habitat (that was sampled at the end of the wet season) (mean=202.24, 95% CI: 165.22—239.26 g/m^2, N=40 plots). The mean grass biomass in Kabini, in both 2015 (mean=706.20 g/m^2, SD=254.302, N=4 months; Welch's U=3.715, df=3.115, P=0.034) and 2016 (mean=583.46 g/m^2, SD=49.752, N=4 months; Welch's U=11.616, df=5.691, P<0.001) was also greater than the mean grass biomass in the adjacent Bandipur National Park (229.4 g/m^2, SD=39.403, N=4 months), reported previously (Devidas 1995, Supplement 4). Although a formal test could not be carried out (Nagarahole forest was sampled within two months), the grass biomass in the forest habitats of the two parks were similar to each other despite being sampled in very different years (Figure 2a, Supplement 4).

1b. *Variation in grass abundance across and within focal zones:* The mixed-effects model explained more than 75% variation in grass biomass, which was found to be unevenly distributed across space and time (Figure 2b). Zone and year x month interaction had moderately large effects on grass biomass, while other factors had low effects if significant (Table 2). Similar trends were obtained for grass cover also (Supplement 4). In the case of grass height, the effect of zone was very large, explaining 47% of the variation, while the effects of year, month x year, zone x year, and zone x year x month interaction were small to moderate (see Supplement 4).

The average within-zone coefficient of variation (CV) was 21% (95% CI: 18.99—23.54, Figure 2c) and average within-plot-cluster CV in grass biomass was 28% (95% CI: 26.13—29.80%, Figure 2d). Similarly, based on grass height, within-zone CV was 22% (95% CI: 18.39—26.06) and within-plot-clusters CV was 30% (95% CI: 28.44—32.30).

2. How do the rates and intensities of individual-level agonism among females compare within and between clans?

We recorded a total of 277 within-clan (duration=173 hours of focal group observations; number of individual-level interactions=459 independent and 267 non-independent interactions) and 96 between-clan (total duration=73 hours of focal group observations; number of individual-level interactions=377 independent and 579 non-independent interactions; no agonism seen in only 8 out of 96 between-clan encounters) focal group observations. Out of these, 180 within-clan (134 hours of focal group observations; 345 independent and 188 non-independent interactions) and 55 between-clan (50 hours of focal group observations; 213 independent and 318 non-independent individual-level interactions; no agonism seen in only 6 out of 55 between-clan encounters) focal group observations were

completely inside the focal zones, were at least 15 minutes long, were independent focal observations (at least 15 minutes apart for within-clan and 2.5 hours apart for between-clan focal group observations), and included feeding as the primary group activity. Therefore, the results on the rate and intensity of individual-level agonism reported below are based on these focal group observations.

The top five commonly observed clans were observed in 39 between-clan and 142 within-clan focal observations, for which we present the results from the mixed-effects models. We found the rate of individual-level agonism per female per hour to be significantly higher during between-clan agonism than in within-clan agonism, and clan identity did not have an appreciable effect (Table 3a, Figure 3a). Similar mixed-effects model based on dyadic rate of agonism also showed that between-clan agonism was more frequent than within-clan agonism (Table 3b).

The rate of individual-level agonism was significantly higher during between-clan agonism than within-clan agonism based on focal observations of all clans also (Figure 3). Based on focal observations from all clans, the average rate of agonism per female during between-clan encounters was 2.441 agonistic interactions/female/hour (95% CI: 1.890—2.993, *N*=55focal group observations) while that within clans was 1.152 agonistic interactions/female/hour (95% CI=0.988—1.316, *N*=180 focal group observations) (Figure 3). The average dyadic rate of agonism during between-clan encounters was 1.069 agonistic interactions/dyad/hour (95% CI=0.827—1.311, *N*=55 focal group observations), while that within clans was 0.414 agonistic interactions/dyad/hour (95% CI=0.343—0.486, *N*=180 focal group observations). The effect sizes of the differences in rates of individual-level agonism between and within clans were large (Cohen's *d*=0.856 for rate of agonism per female, 0.972 for dyadic rate of

agonism). In addition, the comparison of the effect of local competitor density on between-clan and within-clan rates of individual-level agonism showed a significantly steeper slope in the case of between-clan agonism than within-clan inter-individual agonism (Homogeneity of slopes test: type of agonism x number of females effect: $F_{1, 231}$=7.635, P=0.006; β=0.416, 95% CI of β=0.119—0.712, Figure 4).

The intensity of individual-level agonism, measured as the number of non-independent interactions per independent interaction (NI/I ratio), was also higher during between-clan agonism in the fixed effects model using the data for the five common clans (Table 3c). The average NI/I ratio during between-clan agonism, calculated from data from all clans was 1.757 (95% CI=1.296—2.218, N=49 focal group observations with at least one individual-level agonistic interaction) while the average NI/I ratio during within-clan agonism was 0.457 (95% CI=0.328—0.587, N=128 focal group observations with at least one individual-level agonistic interaction). The effect size was large (Cohen's d=1.057, Figure 3b).

3. Is the rate of within-clan agonism explained by variation in grass abundance, grass dispersion, and group size?

Since the random effects of clan identity and year explained negligible variance and resulted in singularity, we present results from fixed effects models. The best-subset model of within-clan rate of agonism per female per hour included female group size, within-plot-cluster grass height, and zone as predictor variables, but explained only about 11% of the variation (Table 4, top models shown in Supplement 6). Female group size and within-plot-cluster height had small effects and were positively related to within-clan rate of agonism (Table 4). A similar examination of the dyadic rate of within-clan agonism also yielded a weak fixed-effects model, explaining only 13% variation, with negative effects of female group size and a

positive effect of within-plot-cluster grass biomass, in addition to significant effect of zones (Supplement 7, top models shown in Supplement 6).

The piece-wise regression of within-clan rate of agonism per female on female group size showed a moderate positive effect until female group size 5 ($F_{1,\ 136}$=19.651, R^2=0.126, P<0.001), and slope not different from zero for the remaining segment ($F_{1,\ 40}$=0.041, R^2=0.001, P=0.841) (Figure 5).

4. Is the rate of individual-level between-clan agonistic interactions explained by variation in grass abundance, grass dispersion, and group size?

The best-subset model of individual-level agonism during between-clan encounters was explained well (*Multiple* R^2=0.517) by month, zone, sum of group sizes of the contesting groups, and within-plot-cluster grass height (Table 5, scatter-plots in Supplement 7, see Supplement 6 for top models). While sum of group sizes was positively related, within-plot-cluster height was negatively related to rate of individual-level agonism during between-clan encounters (Figure 6).

5. Are the rate of clan-level between-clan agonistic encounters and the duration of such encounters related to grass abundance/distribution and group size or the number of clans?

Out of 672 intervals (168 days x 4 intervals, each interval 2.5 hour long), two or more clans were simultaneously present in the focal zone during 91 such intervals (from 56 sampling days), creating the potential for clan-level agonistic encounters. Of these 91 intervals, we observed between-clan agonistic encounters in 30 intervals. The average rate of between-clan agonistic encounters was found to be 0.409 per clan per 2.5-hour interval (95% CI=0.244-0.574), based on 91 intervals. The best-subset model explained 35% of the variation

($F_{1,89}$=47.93, *Multiple* R^2=0.350, P<0.001) in the rate of between-clan agonistic encounters, and showed a strong positive effect of only the number of clans(Table 6, top models shown in Supplement 6, Figure 7a, see Supplement 7 for other scatterplots).

The best-subset regression model of duration of between-clan agonistic encounters (clan level) explained 31% variation (*Multiple* R^2=0.306), with a positive effect of within-plot-cluster average grass biomass and a negative effect of within-plot-cluster average grass cover (Table 7, top models shown in Supplement 6, Figure 7b, see Supplement 7 for other scatter-plots). The partitioning of variances showed that within plot-cluster grass biomass explained 30% of the variation while grass cover explained less than 1% variation in duration of between-clan agonistic encounters (Supplement 6).

Discussion

Despite the ecological model of female social relationships (EMFSR, Wrangham 1980, van Schaik 1989, Isbell 1991) conceptually not being restricted to any taxonomic group, studies on the relationship between food distribution and contest competition in non-primate mammals are almost non-existent. In this study, in a first such test of EMFSR in elephants, we monitored the agonistic interactions among individually identified female Asian elephants to understand the proximate ecological basis of agonistic interactions in the grassland habitat of Kabini. We set out to quantify the relationship between within- and between-clan agonism and food abundance, food distribution, and competitor density effects of group size and number of clans by directly measuring these variables. Since this population showed the occurrence of both between-clan and within-clan agonism despite relying on a graminivorous

diet, which is classified as low quality subsistence food, widely distributed, and assumed not to elicit frequent contests (Wrangham 1980, Archie *et al.* 2006), spatial distribution of food was one of the possible drivers of contest competition. Although forest habitats may have high primary productivity and the forest understorey in the wider landscape has tall-grass areas (Sivaganesan 1991), we found that the grassland in Kabini had about three times the grass biomass as the neighbouring forest habitat of Nagarahole and Bandipur National Parks (data from Bandipur from Devidas 1995). As expected from EMFSR's prediction of between-group contest in high quality patches, we observed frequent occurrence of agonistic between-clan encounters, which was rarely seen in forest habitats previously (Baskaran 1998). Further, consistent with the expectation of EMFSR that high quality resource patches would elicit stronger between-group contest than within-group contest, we found that individual-level agonism was more frequent and intense during between-clan agonism than within-clan agonism. However, in contradiction to EMFSR's prediction of a positive relationship between within-group contest and patchiness of feeding sites, within-clan rate of agonism in our study was not explained by either grass abundance or dispersion at the local level, although we found that female group size (up to intermediate group sizes) positively explained some variation in within-clan agonism, consistent with simplistic models of resource competition. The rate of between-clan agonistic encounters, too, was positively explained by the number of clans present, and the duration of between-clan agonistic encounters was longer when the contest site had greater grass biomass. We discuss our findings on within-clan and between-clan agonism, in the context of their role in shaping the social organization of elephants, as expected from socioecological theory.

Diet and agonism in elephants

We found high between-clan and within-clan agonistic contests among females (see also

Nandini 2016) although only grasses were available as food in the Kabini grassland. The usefulness of diet type as a predictor of contest competition (Wrangham 1980, Isbell 1991, Clutton-Brock and Janson 2012) has been contradicted by observations of within-group and between-group dominance in folivorous primates (for example, Koenig *et al.* 1998, Harris 2006), whose diet was assumed to result in weak contest competition previously (reviewed in Snaith and Chapman 2007). In African savannah elephants also, strong dominance had been observed (Archie *et al.* 2006, Wittemyer and Getz 2007), despite the expectation that contest in elephants would be weak due to their flexible and generalist diet dominated by grasses that were assumed to be widely dispersed (Archie *et al.* 2006). However, Wittemyer and Getz (2007) found that contests among female African savannah elephants were common at point resources such as water holes, trees, and shade. De Silva *et al.* (2017), who found less frequent contests and weaker dominance expression among female Asian elephants in Uda Walawe (Sri Lanka) compared to African elephants of Samburu, argued that higher resource availability in the more mesic habitats of Asian elephants, along with their generalist diet, may facilitate more flexible associations and result in infrequent agonism. Although our study population of Asian elephants also shows flexible associations (discussed below), we found frequent occurrence of agonistic contests in the open grassland (and not for waterholes, trees or shade), which counter earlier interpretations of food distribution from dietary categories as questioned before in the context of primates (Snaith and Chapman 2007, Koenig *et al.* 2009, Wheeler *et al.* 2013). The difference between the Uda Walawe and Kabini populations of Asian elephants in the frequency of agonism is interesting, and it would be interesting to study both the causes (resource distribution) and social consequences (dominance structure) of these differences.

Individual-level agonism within and between clans

Our findings of individual-level between-clan agonism being twice as frequent as within-clan agonism during the observations made when groups were feeding, along with the findings of frequent between-clan agonistic encounters (discussed below), indicate that between-clan contest is strong in the study habitat. Since increased agonism results in the reduction of foraging time and food intake (for example, Janson 1985, Vogel 2005), frequent between-clan agonism, in addition to greater intensity of agonism (higher NI/I ratio), implies that females incur greater foraging costs during between-clan contests as compared to the usual contest competition faced within the clan. The greater slope of the relationship between agonism rates and the number of female competitors implies that greater agonism observed during between-clan encounters is more than what would be expected if an equal number of females from the same clan were present. Moreover, since over 50% of between-clan agonistic encounters in Kabini result in the exclusion of the losing group from the foraging site (Nandini 2016, Gautam and Vidya *unpublished*), there are clear foraging consequences of between-clan agonism, in addition to time lost from such interactions. Greater agonism among females from different clans rather than within the same clans also suggests that females Asian elephants may effectively use agonism as a signal of group membership, which demands advanced cognitive abilities, in addition to the requirements of effective recognition systems in maintaining fission-fusion societies (see Aureli *et al*. 2008).

Clan-level between-clan encounters and Kabini as a resource-rich habitat patch

Although opportunities for between-group competition are high in species with extensively overlapping home ranges, aggressive between-group encounters are thought to be rare in such species, perhaps due to large overlap being associated with low incentives from aggressive defense of territory/ranges (Cheney 1987, Pisor and Surbeck 2019, but see Wrangham 1980

for dominance-based avoidance as a reason for rare between-group aggression), in contrast to species wherein groups show more exclusive ranging that is associated with stronger territorial expression (for example, Willems and van Schaik 2015, see also Brown 2013). Interestingly, our findings of frequent between-clan agonistic encounters suggest that the Kabini grassland has an unusual competition regime. Clans of female Asian elephants are known to have extensively overlapping home ranges (Fernando *et al.* 2008, Baskaran and Desai 1996) and a previous long-term study in the nearby Mudumalai forest in the Nilgiri Biosphere Reserve in southern India (Baskaran 1998, Baskaran *et al.* 2018 discussed below) and in Sri Lanka (Prithiviraj Fernando, *personal communication*, see also de Silva *et al.* 2017) have rarely observed between-clan agonistic encounters. The high percentage (91.7%) of aggressive between-clan encounters (88 out of 96 between-clan encounters were agonistic) observed in Kabini is also higher than that reported in primates that show extensive home range overlap (between-group encounters are rarely aggressive, but occasionally, up to 69% of between-group encounters may be aggressive in species with ~50% or more overlap, reviewed in Cheney 1987, see also Cooper *et al.* 2004, Mirville *et al.* 2018), although the consequences of aggression can be more lethal in primates. This strong between-clan contest competition in Kabini can be explained by the peculiar food distribution in our study area. We found that the small Kabini grassland is a food-rich habitat compared to forests in Nagarahole, where grass is scarce in the lean season, and savanna-woodland/forest in Bandipur National Park based on previous data (Devidas 1995) (Supplement 4). This concentration of resources (including water) in Kabini is reflected in the exceptionally high elephant density observed in Kabini during the sampling period (Supplement 4). Given the high quality nature of the grassland habitat at Kabini, frequent between-clan agonism is consistent with the expectations of strong between-group contest for high quality resource patches for species with extensive home range overlap (Wrangham 1980, see also Brown

2013). Strong between-group contest is thought to have implications for sociality as EMFSR predicts larger groups to be advantageous. Consequently, greater within-clan tolerance of subordinates by the dominant females is required to maintain large groups (Sterck *et al.* 1997). Data from the Kabini Elephant Project suggests that larger groups are more likely to win between-clan contests (Nandini 2016, Gautam and Vidya *unpublished*) and, in the future, it would be interesting to see if, due to strong between-clan contest, within-clan tolerance and social cohesion are greater in the Kabini grassland than in forests.

Correlates of within-clan agonism

Although we observed within-clan agonism frequently, it did not conform to EMFSR's classical prediction of more frequent agonistic contests in places with more heterogeneous food distribution, as the rate of agonism was not positively correlated with local variability (within-plot-cluster CV) in grass biomass. One explanation for this could be that feeding competition in our study area is very intense, arising due to the unusual nature of resource distribution at a larger spatial scale as explained in the section above. Female density in the grassland habitat is also much higher than the overall female density in Nagarahole and Bandipur National Parks (Supplement 4), indicating a temporary habitat saturation during the dry season. Resource concentration in this small grassland habitat in the lean season, along with high elephant density, could result in very high overall feeding competition in the grassland to the point where local variations in food dispersion do not have much influence on within-clan agonism. Individuals might be adopting a tactic of maximizing the access to any feeding site through agonistic contests under extreme competition. Such high competition in the unusual habitat setting created due to construction of a reservoir reinforces previous concerns about human interferences affecting social systems of wild populations (see Sterck *et al.* 1997, Halliwell *et al.* 2017, He *et al.* 2019, see also Robbins and Robbins 2018).

Collared clans would have to be followed in order to find out what the patterns of agonism are in forest habitat.

One cannot rule out the possibility that the methodology with respect to measuring grass dispersion could have resulted in the absence of a positive association between within-clan agonism and food distribution in the grassland habitat. Although the spatial extent of measurement of grass dispersion within plot-clusters (inter-quadrat distances from random sampling) was of the same order of magnitude as elephant group spread, it is possible that the distances used are not the best suited to the scale at which feeding competition operates between individual elephants. Future studies could develop consumer-defined measures of food dispersion (for example, focal tree sampling, Vogel and Janson 2011), although this might be challenging in grassland habitats where food is continuously spread with no reference points, unlike in the case of most primates whose foraging patches may be more distinguishable (canopy spread and trunk position used as reference points). Relevant aspects of elephant foraging such as average group spread and inter-individual distances during foraging would also have to be considered during such sampling. One of our future objectives is to explore consumer-based measures of food distribution such as food-site depletion and residence time to understand contest competition (for example, Chapman *et al.* 1995, Chancellor and Isbell 2009).

The observed positive relationship between within-clan agonism rate and female group size was expected from simple models of competition. Since group size represents local density of competitors for a focal individual, larger groups face greater within-group contest when feeding sites are limited (Koenig and Borries 2006). This has been reported many times before in primates (see van Schaik *et al.* 1983, Wittig and Boesch 2003, Klass and Cords

2015, Wheeler *et al.* 2013) although not in elephants. Increase in agonism with group size suggests ecological constraints on larger groups, which had also been suggested previously in this population based on average group sizes not differing across clans despite differences in clan sizes and reduced average association strength in larger clans (Nandini *et al.* 2018). Higher agonism in larger groups implies that, although larger group size may confer feeding benefits in this habitat with strong between-clan contest regime (see above), a part of such foraging benefits accruing from larger group size are offset by the costs of higher within-clan contest as group size increases, possibly in addition to the usual expectation of increased within-group scramble (ecological constraints model, Wrangham *et al.* 1993, Chapman *et al.* 1995).

While dealing with the proximate costs of larger group size, previous studies have looked at the feeding (faster food depletion) and energetic (movement costs) consequences arising largely from exploitative (scramble) competition, as evident from the literature on ecological constraints models (Wrangham *et al.* 1993, Chapman *et al.* 1995, see also Snaith and Chapman 2007, Smith *et al.* 2008). However, within-group contest, too, can have non-trivial consequences such as loss in foraging opportunities and physiological (stress) costs that can influence sociality (reduced within-group tolerance and cooperation, permanent group fissions, see Sterck *et al.* 1997). Thus, studies that account for the effects of both scramble and contest competition could add to our understanding of proximate mechanisms governing group size, which has shown different relationships with foraging efficiency, travel costs and stress in different populations (Markham *et al.* 2015, Grueter *et al.* 2018). In our results from piece-wise regression of rate of agonism on group size, while the absence of a positive relationship in the segment after group size of 5 could be seen as conforming to a non-linear relationship (for example, Grueter *et al.* 2018 on gorillas) in a strong between-clan

competition regime, our sample size for large group sizes was low. In the future, it might be worth exploring such non-linearity in the foraging costs and benefits of larger group size in this habitat. The dyadic rates of agonism showing a negative effect of group size is consistent with the comparative study on primates by Cowl and Shultz (2016). Cowl and Shultz (2016) found a positive relationship between dyadic agonism and collective action, and suggested that the negative relationship between dyadic rates of agonism and group size (from reducing agonism towards other group-mates) could mediate the maintenance of prosocial relationships.

Correlates of clan-level between-clan agonism

The rate of (clan-level) between-clan agonistic encounters showed a strong positive effect of the number of clans but was not related to within-zone grass biomass even though zones differed greatly in grass biomass. However, the duration of between-clan agonistic encounters, a variable that may reflect intensity of contest (Roth and Cords 2016), was positively explained by local grass biomass, which is consistent with game theory explanations of contests becoming longer when the resource value of contest location is high (Smith and Parker 1976). In the socioecological framework, whether food abundance or patchiness shapes between-group contest has been a topic of interest, the answer to which has remained elusive due to scarcity of empirical data (Koenig 2002). Our study provides positive results with respect to food abundance, which explained the duration of agonistic between-clan encounters, in addition to habitat-level differences in grass biomass explaining strong between-clan contest. Studies on primates have found more between-group contests when food abundance was high or when intensity of feeding at a location was high (Wilson *et al.* 2012, Brown 2013, Pal *et al.* 2018), suggesting the role of food abundance in between-group contest (see also Harris 2006, Roth and Cords 2016). In addition to the effect of the resource

value of contest site, the resource holding potential of the contestants is also thought (Smith and Parker 1976) to determine the duration and intensity of contests, which can be applied to group-level contests also (for example, Markham *et al.* 2012). While previous studies on primates (for example, Roth and Cords 2016, Mirville *et al.* 2018) have found that between-group contests last longer and are more intense if competing groups are evenly matched in group size (a proxy for groups' resource holding potential), we did not find any effect of the difference in group size on contest duration. It is possible that this could result from the participation of sub-adult females or males in between-clan contests, which was not explored in this study, or because of non-participation by some group members, which could affect the collective defense of resources. These remain to be explored in the future.

Fission-fusion sociality and within-clan agonism

Fission-fusion sociality is expected to confer flexibility in grouping behavior to balance the costs and benefits of large social groups in response to environmental variability across space and time (Aureli *et al.* 2008, see also Sueur *et al.* 2011). Interestingly, our study found frequent within-clan agonism which would seem surprising since there is flexibility in associations among females in the Kabini population (Nandini *et al.* 2017, 2018). An explanation for high within-clan contest in Kabini could be the need to be in larger groups due to between-clan contest being strong, as discussed above. The advantage of larger groups is supported by the previous findings on the observed female group size being higher in the grassland than in the adjacent forests (Vidya *et al. unpublished*). In another study, de Silva *et al.* (2017) had ascribed lower agonism among female Asian elephants observed in Uda Walawe, in contrast to African savannah elephants in Samburu (Wittemyer and Getz 2007), to conditions that facilitate greater fission-fusion, namely higher resource availability due to mesic environment and lower predation risk in Asian elephant habitats. A testable hypothesis

to explain lower agonism found by de Silva *et al.* (2017) would be the expectation of greater resource availability in the tall-grass grassland habitat of Uda Walawe and more similarity between that grassland and the neighbouring forest, in comparison to Kabini grassland and Nagarahole forests.

Lastly, the findings of our study must be seen in the light of such grassland habitats around the man-made reservoirs being recently created habitats, and not the natural habitat (forests/savannah woodlands) of Asian elephants. Hence, the patterns of high within-clan and between-clan contest reflect plastic responses to such novel environments, and may not reflect the basal or adaptive behavior in more pristine natural habitats. For the latter, similar quantitative studies of agonistic interactions in the forest habitats will be crucial to understanding sociality in female Asian elephants.

Conclusion

A consistent trend in our study was that local competitor density positively affected the rate of agonism at both individual (female) and clan level. This suggests that despite higher abundance of grass, feeding competition is very high in Kabini. These results conform to the broader socioecological framework (van Schaik 1989) where between-group contest is expected to be stronger at higher animal density, which is supported by few studies (for example, Kumara *et al.* 2014). Another implication of high within-clan agonism on social relationships, according to predictions of EMFSR, would be a strongly expressed dominance hierarchy, and consequently, strong rank-related skew in foraging success within groups (Janson and van Schaik 1988). De Silva *et al.* (2017) found agonism to be rare in the Uda Walawe population in Sri Lanka and found a weak expression of dominance relationships. But, interestingly in our population, despite frequent occurrence of agonism, our analyses of

the dominance structure (see also Nandini 2016) and a test of the relationship between dominance rank and grass abundance at foraging sites in this habitat during the same period does not support this prediction (Gautam and Vidya 2019). This makes the Kabini population an interesting contradiction to predictions of EMFSR, which may require alternative explanations (Gautam and Vidya 2019, see also Koenig and Borries 2009).

In conclusion, our tests of some predictions of EMFSR in female Asian elephants show that food distribution explains between-clan contest better than within-clan contest and that competitor density increases both within-clan and between-clan contest. While between-clan agonism conforms to EMFSR, we had limited success in explaining within-clan agonism, which might also be examined profitably using alternate methods of measuring food dispersion and usurpability in future. We call for more field-based studies of proximate ecological basis of agonistic contests, dominance relationships, and their consequences in other populations of elephants to tests the generality of socioecological models in the Proboscidean clade and other mammal species.

Acknowledgements

This work was funded by the Department of Science and Technology's (Government of India) Ramanujan Fellowship to TNCV under Grant No. SR/S2/RJN-25/2007 (dated 09/06/2008), Council of Scientific and Industrial Research, Government of India, under Grant No. 37(1375)/09/EMR-II and No. 37(1613)/13/EMR-II, National Geographic Society, USA, under Grant #8719-09 and #9378-13, and JNCASR. JNCASR provided logistic support. HG thanks JNCASR for a Ph.D. scholarship and institutional support. This work is part of HG's

thesis. We are grateful to the office of the PCCF, Karnataka Forest Department, the office of the Conservator of Forests and Director, Rajiv Gandhi National Park, Hunsur, and other officials for field permits, and various officials and staff of Nagarahole National Park for support at the field site. We thank Amitabh Joshi, JNCASR, for advising us on ANOVAs of grass abundance. We thank Revathe T. for help during data collection and Manan Gupta for helping with MATLAB codes to sort clan-visits data. We thank Shankar, Krishna, Ranga and Pramod for field assistance and ensuring our safety in field.

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Figure legends

Figure 1. a) Maps showing the location of Nagarahole and Bandipur National Parks and the Kabini backwaters between them, in southern India. The rectangle placed in the centre highlights the backwaters area which is an open grassland during the dry season. b) Map of the Kabini backwaters area showing the outlines of the six focal zones (grey dot-filled polygons) sampled in the grassland habitat (in grey). c) An illustration of the sampling scheme used to sample grass abundance, showing five quadrats each in four plot-clusters in a focal zone.

Figure 2. Grass biomass and distribution at different scales: a) grass abundance in the forest (Forest-N refers to Nagarahole National Park and Forest-B refers to Bandipur National Park) and grassland habitats around the backwaters, b) grass abundance (mean ± 95% CI estimated from averages of 4 plot-clusters) in different focal zones of the grassland habitat in different months of 2015 and 2016, c) within-zone CV in grass biomass (estimated from four plot-clusters) indicating variability across different plot-clusters within the focal zones, and d) within-plot-cluster CV in grass biomass (estimated from five quadrats), indicating local variability in grass abundance.

Figure 3. a) Rates of individual-level agonism per female per hour observed during between-clan and within-clan focal group observations of five common clans, b) rates of individual-level agonism (per female per hour and per dyad) observed during between-clan and within-clan focal group observations of all clans, and c) intensity of individual-level agonism (number of non-independent agonistic interactions per independent agonistic interaction between two females) during between- and within-clan interactions.

Figure 4. Overlaid scatterplots and slopes of rate of individual-level agonism during within-clan (open circles, dashed line) and between-clan (filled diamonds, solid line) focal group observations with respect to the number of female competitors (group size in the case of within-clan and sum of group sizes in the case of between-clan agonism).

Figure 5. Piece-wise regression to show the relationship between female group size and within-clan rate of agonism per female for group size segments 2-5 and greater than five. Each data point in the graph is a focal group observation. Since many data points overlap on the graph, the median within-clan rate of agonism corresponding to each group size is also shown.

Figure 6. Scatterplots showing the effects of a) the sum of group sizes and b) within-plot-cluster grass height on individual-level agonism per female per hour during between-clan agonism.

Figure 7. Scatterplots showing the effects of a) the number of clans on clan-level between-clan agonistic encounters, and d) within-plot-cluster grass biomass on the duration of clan-level between-clan agonistic encounters.

Tables

Table 1. Formulae used to calculate a) the rate of agonism per female per hour (*sensu* Wheeler *et al.* 2013) and dyadic rate of agonism per hour (*sensu* Cowl and Shultz 2017) to compare individual-level agonism from each focal observation on within- or between-clan encounters, and b) the rate of clan-level between-clan agonistic encounters in each focal zone. In the case of individual-level agonism (within or between clans), I = number of independent individual-level agonistic interactions observed in a focal observation, t = duration of focal group observation, n=group size (for within-clan agonism), $n1$ and $n2$ = group sizes of the competing groups (for between-clan agonism). For the rate of clan-level agonism between-clans, I = number of agonistic between-clan encounters per 2.5-hour interval in a focal zone, N = number of clans in the focal zone during the corresponding interval.

	a) Individual-level agonistic interactions	
	Rate of agonism per female	Dyadic rate of agonism
Within-clan agonism	$\frac{2 \text{ x } I}{n \text{ x } t}$	$\frac{2 \text{ x } I}{n\,(n-1) \text{ x } t}$
Between-clan agonism	$\left[\frac{I}{n1 \text{x } t} + \frac{I}{n2 \text{ x } t}\right]/2$	$\frac{I}{(n1 \text{ x } n2) \text{ x } t}$
	b) Clan-level between-clan agonism	
Clan-level between-clan agonism	$\frac{2 \text{ x } I}{N}$	

Table 2. Results from the mixed-effects GLM showing the effects of year (random factor), month and zones (both fixed factors), and their interactions on grass biomass (g/m^2). Significant (<0.05) *P* values and effect sizes above 0.2 are marked in bold.

Effect (Fixed/ Random)	SS	df_1	MS (effect)	df_2	MS (denom.)	*F*	*P*	Effect size (η^2)
Intercept	79717697.606	1	79717697.606	1	712018.848	111.960	0.060	
Year (R)	712018.848	1	712018.848	144	18548.337	38.387	**<0.001**	0.060
Month (F)	1519393.630	3	506464.543	3	1096869.867	0.462	0.729	0.127
Zone (F)	2687043.475	5	537408.695	5	15744.631	34.133	**<0.001**	**0.225**
Month x Year (R)	3290609.600	3	1096869.867	144	18548.337	59.136	**<0.001**	**0.275**
Zone x Year (R)	78723.155	5	15744.631	144	18548.337	0.849	0.517	0.007
Month x Zone (F)	432191.377	15	28812.758	15	38093.637	0.756	0.702	0.036
Zone x Month x Year (R)	571404.559	15	38093.637	144	18548.337	2.054	**0.015**	0.048
Error	2670960.468	144	18548.337					**0.223**
Corrected Total SS	11962345.112							

Table 3. Results from a) mixed effects model testing the effect of type of agonism (between-clan/within-clan, fixed effect) and clan identity (random effect) on the rate of individual-level agonism per female per hour, b) mixed effects model testing the effect of type of agonism (between-clan/within-clan, fixed effect) and clan identity (random effect) on the dyadic rate of individual-level agonism per female per hour, and c) fixed effects model testing the effect of type of agonism (between-clan/within-clan) on NI/I ratio. These results are for five common clans. Significant *P* values are marked in bold. In mixed effects models, R^2 (marginal) includes only the fixed effects, whileR^2 (conditional) also includes the variance explained by random effects.

Fixed/ Random	Effect	Estimate	S.E. of estimate	95% CI of estimate		*t*	*P*
a)							
Fixed	Intercept	2.221	0.183	1.862	2.580	12.134	**<0.001**
Fixed	Type of agonism: within-clan	-1.217	0.207	-1.623	-0.810	-5.868	**<0.001**
Random variation							
Random effect (intercept)	Clan identity (*N*=5): variance = 0.031						
Residuals	Residual variance (*N*=218) = 2.110						
	R^2(m), R^2(c)	0.138, 0.150					

Fixed/ Random	Effect	Estimate	S.E. of estimate	95% CI of estimate		*t*	*P*
b)							
Fixed	Intercept	0.994	0.078	0.840	1.147	12.678	**<0.001**
Fixed	Type of agonism: within-clan	-0.620	0.093	-0.802	-0.438	-6.675	**<0.001**
Random variation							
Random effect (intercept)	Clan identity (*N*=5): variance = 0.003						
Residuals	Residual variance (*N*=218) = 0.427						
	R^2(m), R^2(c)	0.171, 0.177					
c)							
Fixed	Intercept	1.713	0.154	1.411	2.016	11.105	**<0.001**
Fixed	Type of agonism: within-clan	-1.267	0.203	-1.665	-0.870	-6.247	**<0.001**
Random variation							
Random effect	Clan identity: variance = NA						
Residual S.E. (*df*=164)			1.291				
	Multiple R^2	0.192					

Table 4. Results from the best-subset fixed-effects model explaining within-clan rate of individual-level agonism per female per hour. Significant *P* values are marked in bold.

Fixed/ Random	Effect	Estimate	S.E. of estimate	95% CI of estimate		*t*	*P*
Fixed	Intercept	-0.035	0.383	-0.781	0.711	-0.091	0.927
Fixed	Group size	0.106	0.039	0.029	0.182	2.703	**0.008**
Fixed	Within-plot-cluster height	0.134	0.051	0.035	0.233	2.634	**0.009**
Fixed	Zone- KKU	0.462	0.366	-0.252	1.176	1.261	0.209
Fixed	Zone- MK	-0.492	0.299	-1.075	0.091	-1.646	0.102
Fixed	Zone- NB	-0.354	0.328	-0.993	0.286	-1.078	0.283
Fixed	Zone- RKB	-0.071	0.223	-0.505	0.364	-0.317	0.751
Fixed	Zone- TH	0.687	0.306	0.090	1.283	2.245	**0.026**
Residual S.E. (*df*=166)			1.090				
	Multiple R^2	0.111					

Table 5. Results from the best-subset fixed-effects model explaining the rate of individual-level between-clan agonistic interactions. Significant *P* values are marked in bold.

Fixed/ Random	Effect	Estimate	S.E. of estimate	95% CI for estimate		*t*	*P*
Fixed	Intercept	2.906	1.214	0.539	5.273	2.394	**0.021**
Fixed	Sum of group sizes	0.382	0.109	0.169	0.596	3.499	**0.001**
Fixed	Within-plot-cluster height	-0.408	0.176	-0.751	-0.064	-2.315	**0.025**
Fixed	Zone- KKU	-4.527	1.302	-7.065	-1.988	-3.478	**0.001**
Fixed	Zone-MK	-0.811	1.274	-3.295	1.673	-0.637	0.528
Fixed	Zone- NB	-2.137	1.229	-4.533	0.259	-1.739	0.089
Fixed	Zone- RKB	-0.299	0.586	-1.442	0.843	-0.511	0.612
Fixed	Month- Feb	-0.570	0.552	-1.646	0.506	-1.033	0.308
Fixed	Month- Mar	1.253	0.754	-0.217	2.723	1.662	0.104
Fixed	Month- May	4.378	0.889	2.644	6.111	4.925	**<0.001**
Residual S.E. (*df*=43)			1.525				
	Multiple R^2	0.517					

Table 6. Results from the best-subset linear model (all fixed effects) explaining the rate of clan-level between-clan agonistic encounters per clan per 2.5-hour interval. Significant *P* values are marked in bold.

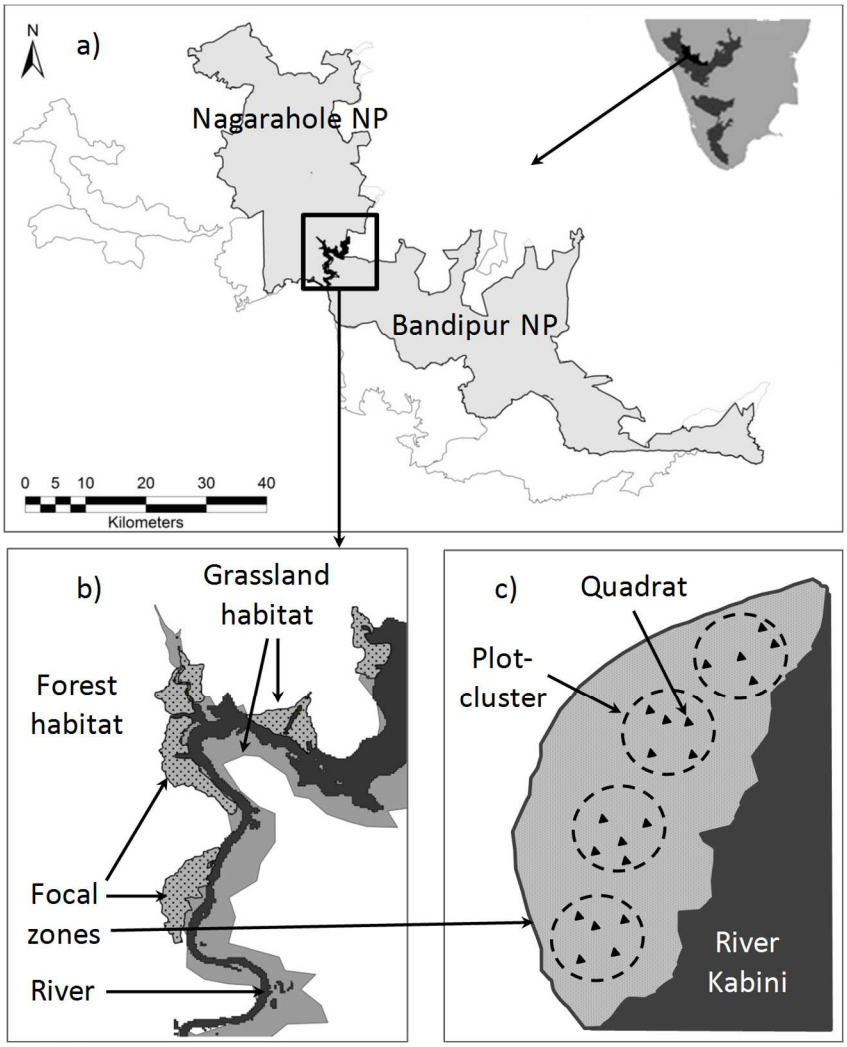
Fixed/ Random	Effect	Estimate	S.E. of estimate	95% CI for estimate		*t*	*P*
Fixed	Intercept	-0.826	0.191	-1.198	-0.453	-4.323	**<0.001**
Fixed	No. of clans	0.461	0.067	0.331	0.590	6.923	**<0.001**
Residual S.E. (*df*=89)			0.651				
	Multiple R^2	0.350					

Table 7. Results from the best-subset model explaining the duration of between-clan agonistic encounters. Significant *P* values are marked in bold.

Fixed/ Random	Effect	Estimate	S.E. of estimate	95% CI for estimate		*t*	*P*	η^2
Fixed	Intercept	289.871	99.776	95.307	484.435	2.905	0.006	-
Fixed	Within-plot-cluster biomass	0.161	0.036	0.091	0.232	4.459	0.000	0.300
Fixed	Within-plot-cluster cover	-3.813	1.197	-6.147	-1.479	-3.186	0.003	0.007
Residual S.E. (*df*=46)			35.51					
	Multiple R^2	0.306						

Figures

Figure 1.



1 Figure 2.

2

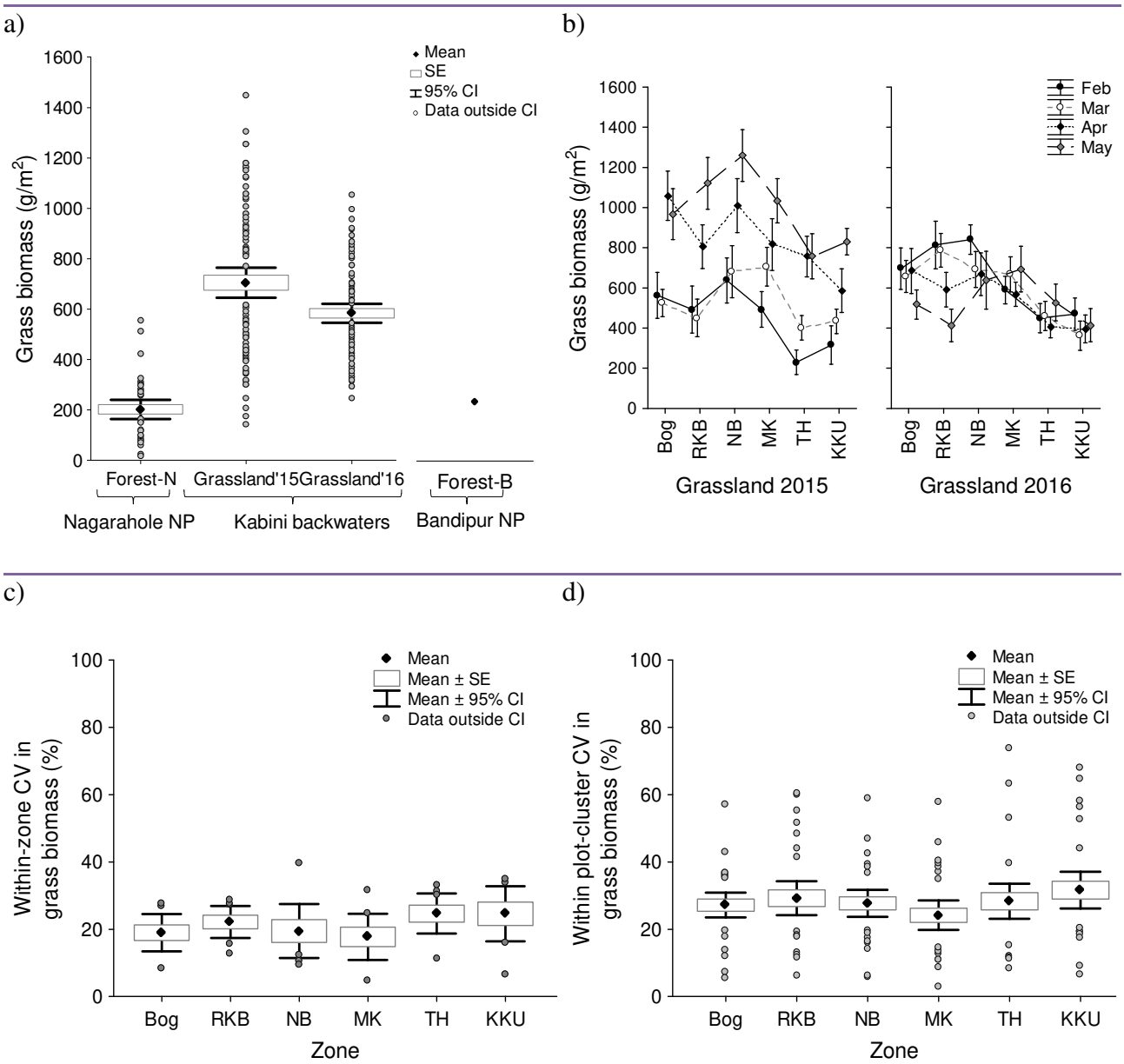


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Figure 3.

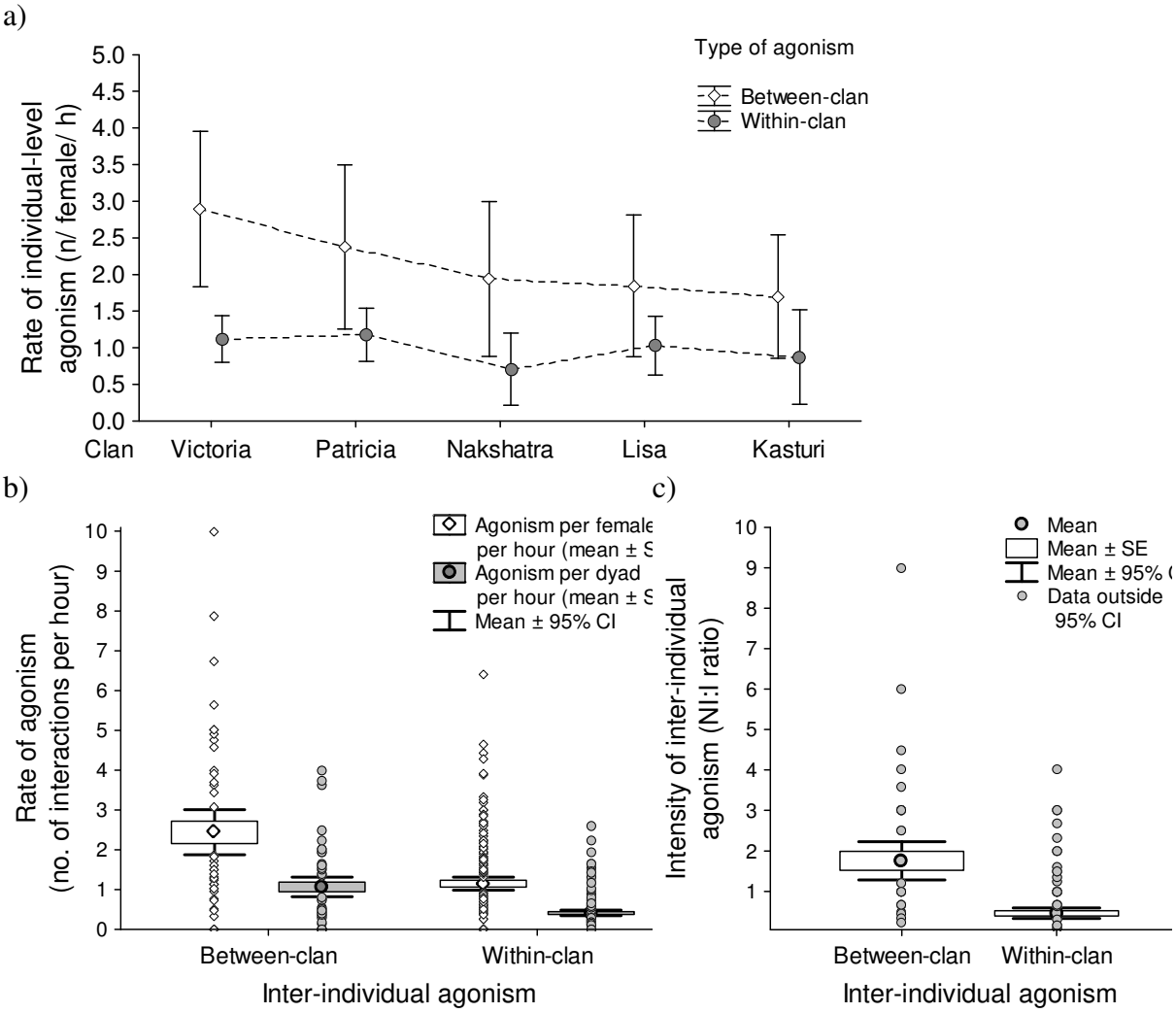
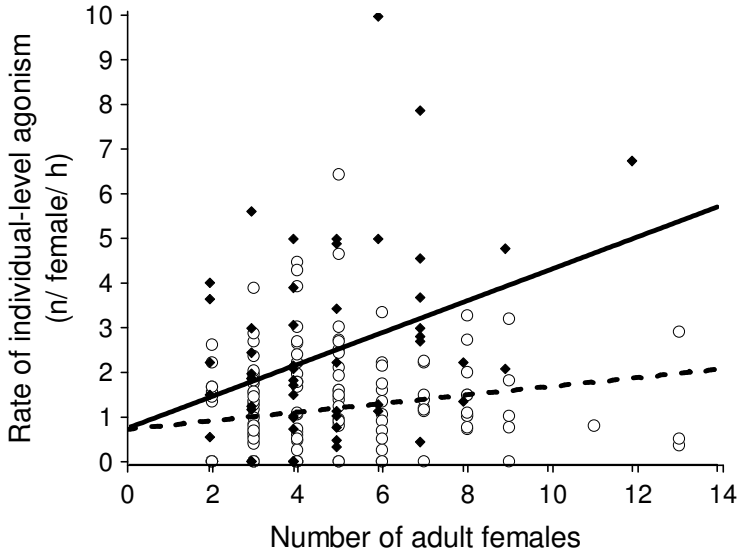
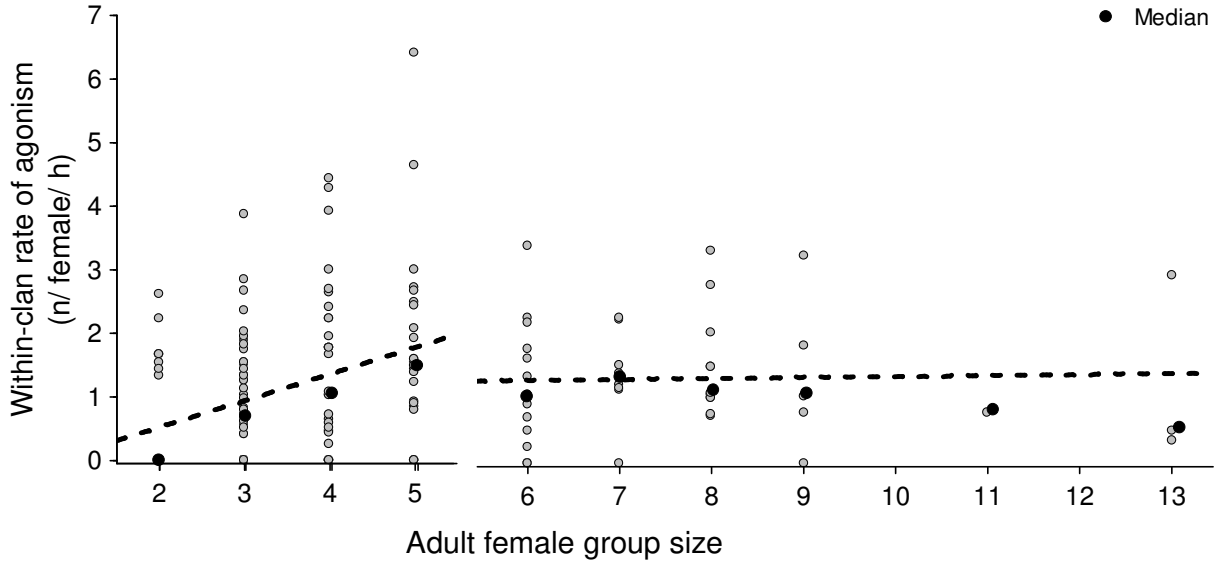

a)
Type of agonism
Between-clan
Within-clan
Rate of individual-level agonism (n/ female/ h)
5.0
4.5
4.0
3.5
3.0
2.5
2.0
1.5
1.0
0.5
0.0
Clan
Victoria
Patricia
Nakshatra
Lisa
Kasturi
b)
Agonism per female per hour (mean ± S
Agonism per dyad per hour (mean ± S
Mean ± 95% CI
Rate of agonism (no. of interactions per hour)
Between-clan
Within-clan
Inter-individual agonism
c)
Mean
Mean ± SE
Mean ± 95% C
Data outside 95% CI
Intensity of inter-individual agonism (NI:I ratio)
Between-clan
Within-clan
Inter-individual agonism

Figure 4.


Rate of individual-level agonism
(n/ female/ h)
10
9
8
7
6
5
4
3
2
1
0
0
2
4
6
8
10
12
14
Number of adult females

1 Figure 5.

2



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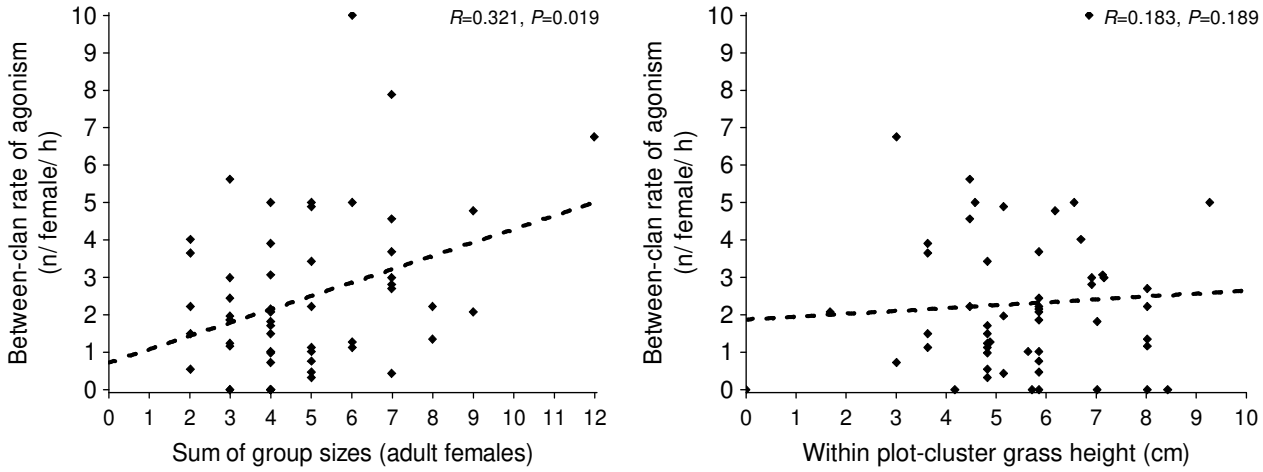
1 Figure 6.

2

a) b)



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1 Figure 7.

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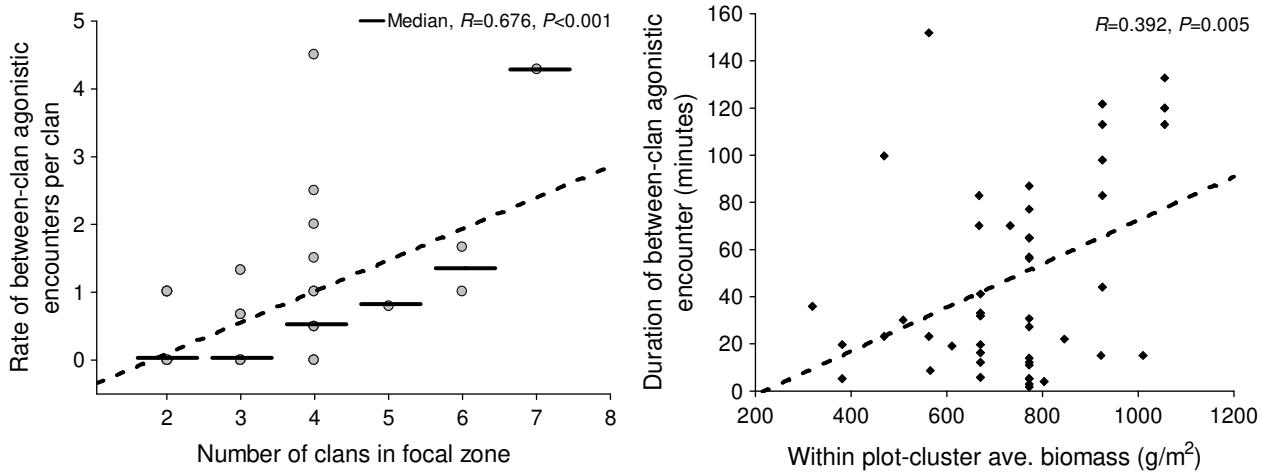
a) b)



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Supplement 1. Pictures of the grassland habitat around the Kabini backwaters, foraging elephant groups, and a few agonistic interactions.

Supplement 1, Figure 1. Elephants foraging in the grassland habitat around the Kabini backwaters.

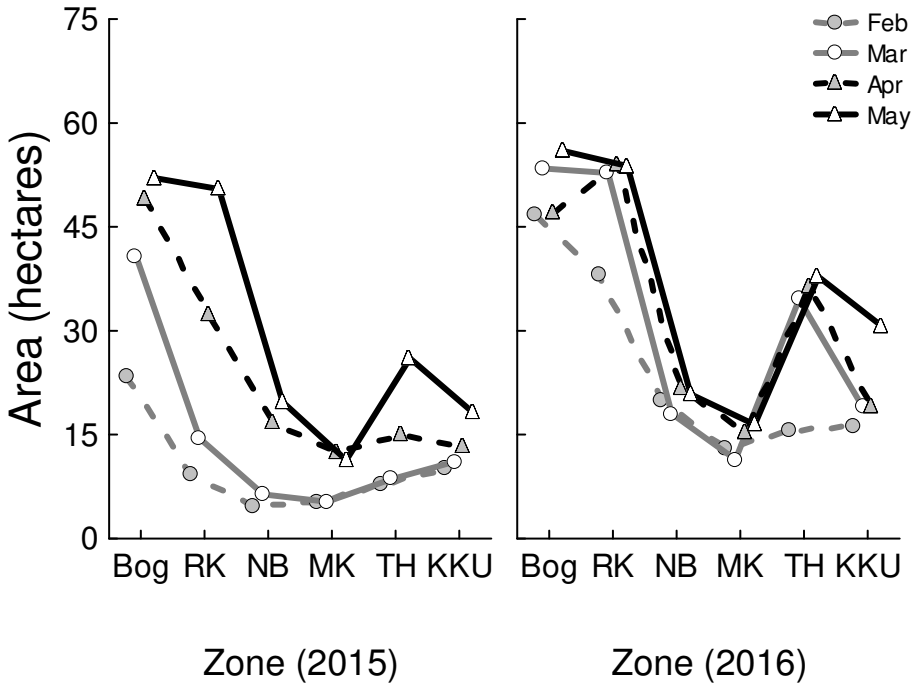
Supplement 1, Figure 2. An elephant group feeding in the RKB (Rajamanakere backwaters) focal zone of the grassland habitat in Kabini. The background shows the edge of the forest.

Supplement 1, Figure 3. An agonistic interaction (hit) during a between-clan agonistic encounter involving Sunetra (initiator of agonism) and other members of Victoria's clan, and Nandini (recipient) and other members of Nakshatra's clan.

Supplement 1, Figure 4. Another individual-level agonistic interaction (trunk on head) during a between-clan agonistic encounter, involving Sunetra (initiator of agonism) from Victoria's clan and Nandini (recipient) from Nakshatra's clan.

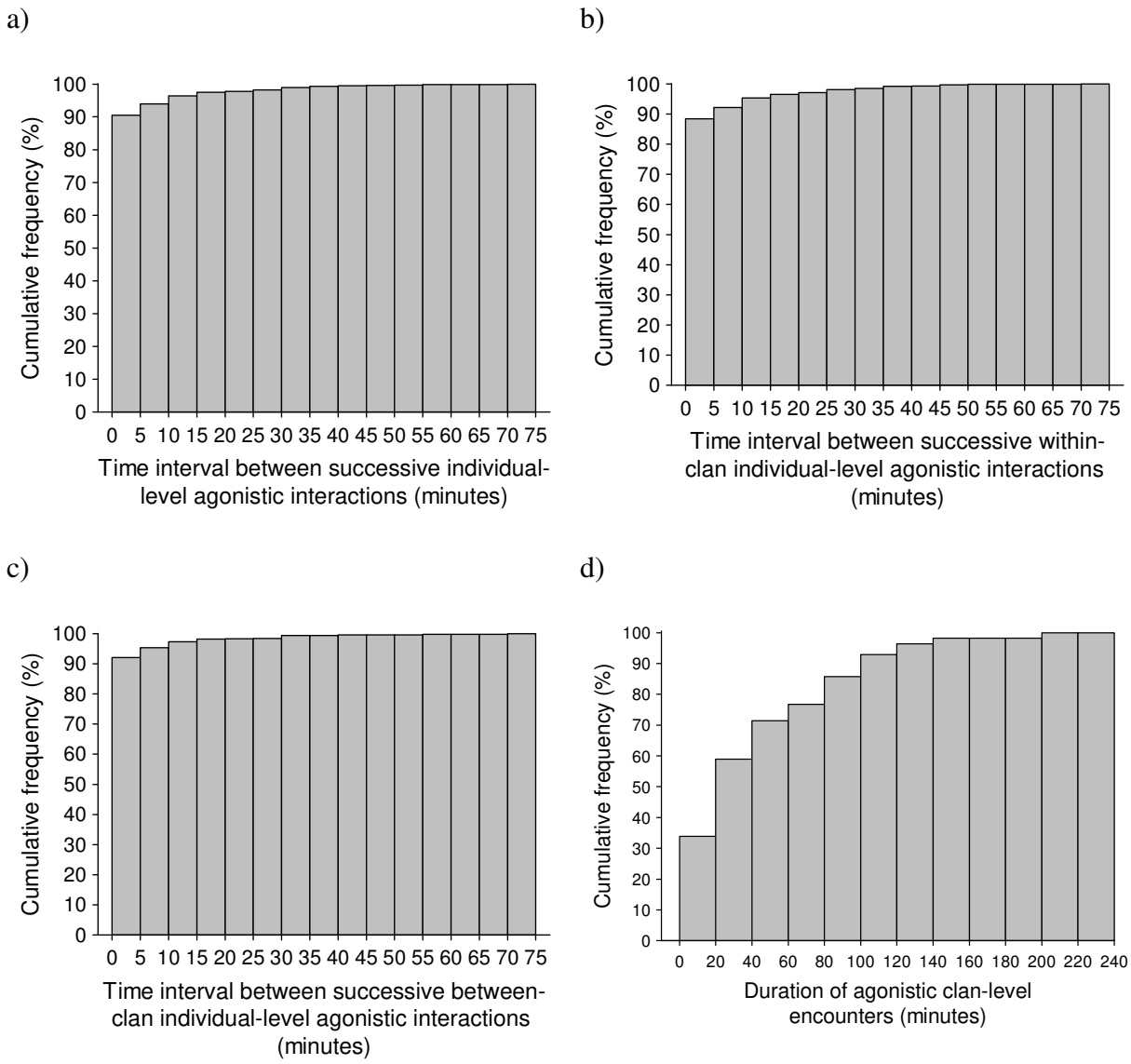
Supplement 1, Figure 5. A 1 m x 1 m quadrat, from which grass biomass has been harvested from the ground level.

Supplement 2. Areas of focal zones sampled.



Supplement 2, Figure 1. Areas of focal zones during different dry season months of 2015 and 2016. Each area was calculated by delineating water and forest boundaries of each focal zone using monthly Landsat 8 satellite images. The areas varied across months due to fluctuations in the reservoir's water level.

Supplement 3. Time interval between successive individual-level agonistic interactions and duration of clan-level agonistic encounters.



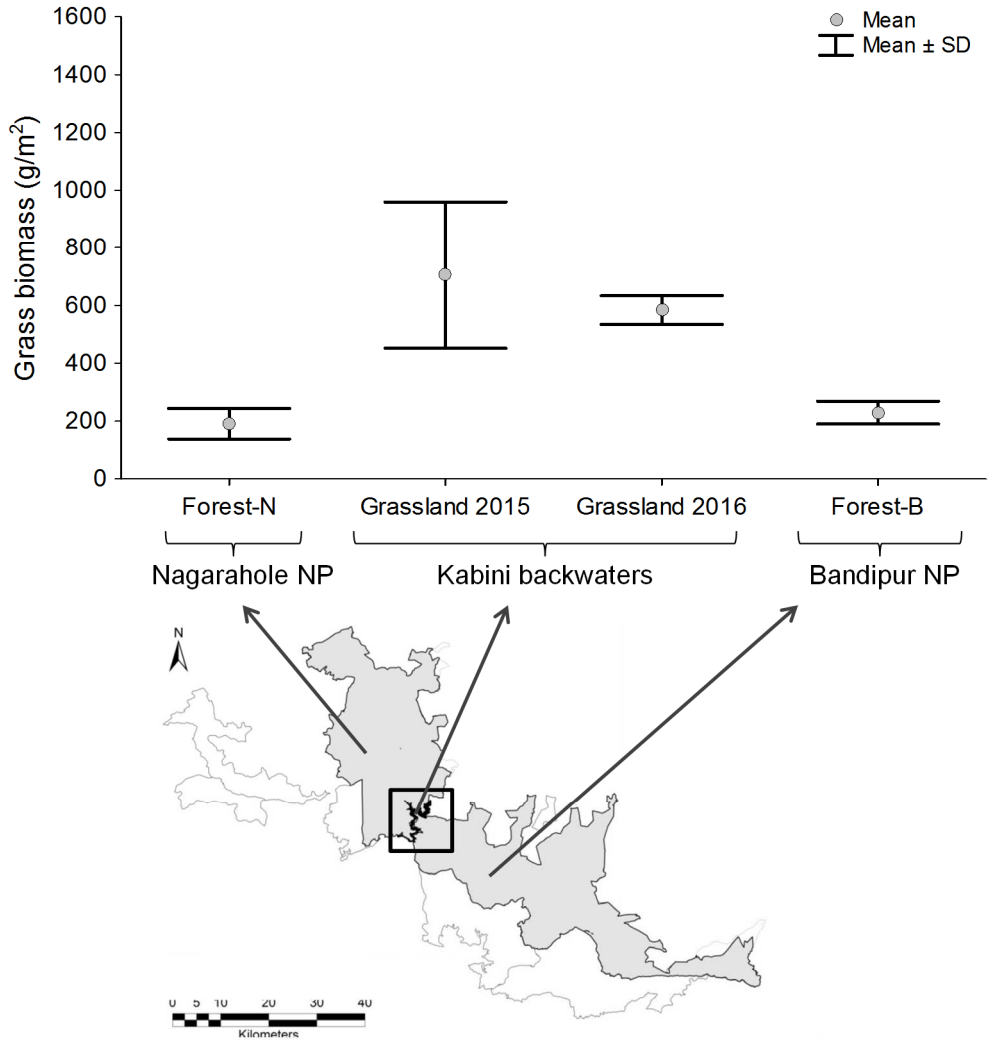
Supplement 3, Figure 1. a) Cumulative frequency distribution of the time interval between successive individual-level agonistic interactions for all (within-clan and between-clan) individual-level agonistic interactions (*N*=1682). Time interval between successive individual-level agonistic interactions was calculated by subtracting the time of occurrence of each interaction occurring between two females in the focal duration from that of the

subsequent interaction involving the same females during that focal observation. Data from the first figure were further divided into b) time interval between successive within-clan individual-level agonistic interactions (*N*=726) and c) time interval between successive between-clan agonistic interactions (*N*=956). Since over 95% of successive interactions (during both within-clan and between-clan agonism) occurred within 15 minutes, we eventually used 15 minutes as the cutoff to define an independent interaction for data analyses. The last column in a), b), and c) represents an interval of 75 minutes or more. d) Cumulative frequency distribution of the duration of between-clan agonistic encounters (at the clan-level), calculated from the start and end time of each agonistic encounter. Based on this, we used a 2.5 hour cut off to demarcate consecutive encounters between the same groups as independent focal observations for the purpose of calculating the rate of individual-level agonistic interactions during between-clan agonism. We also divided the sampling day into 2.5-hour intervals to count the occurrence of between-clan encounters in a focal zone and calculate the rate of between-clan agonistic encounters (clan-level rate).

Supplement 4. Grass biomass in the grassland habitat in Kabini and in the neighbouring forest/savannah woodland habitats of Nagarahole and Bandipur National Parks, and variability in grass cover, grass height, and density of elephants around the Kabini backwaters.

As mentioned in the main text, we compared the grass biomass in the grassland habitat in Kabini with that in the neighbouring forest/savannah woodland habitats of Nagarahole and Bandipur National Parks. The mean and SD of monthly values in the four cases, which were used to perform the Welch's test, are shown in Figure 1 below. In Bandipur, the savannah-woodland habitat of Ainurmarigudi Range had been sampled and grass biomass values averaged from the monthly wet phytomass of grasses from February to June of 1993 by Devidas (1995, pp.71). The monthly values of wet grass phytomass were 261.61 g/m^2 in February, 180.25 g/m^2 in March, 198.61 g/m^2 in April, 234.72 g/m^2 in May, and 271.6 g/m^2 in June.

The results of the GLMs to examine the variability in grass cover and grass height in the Kabini grassland, and the within-day temporal profile of the density of adult females in the focal zones are also shown in this Supplement.



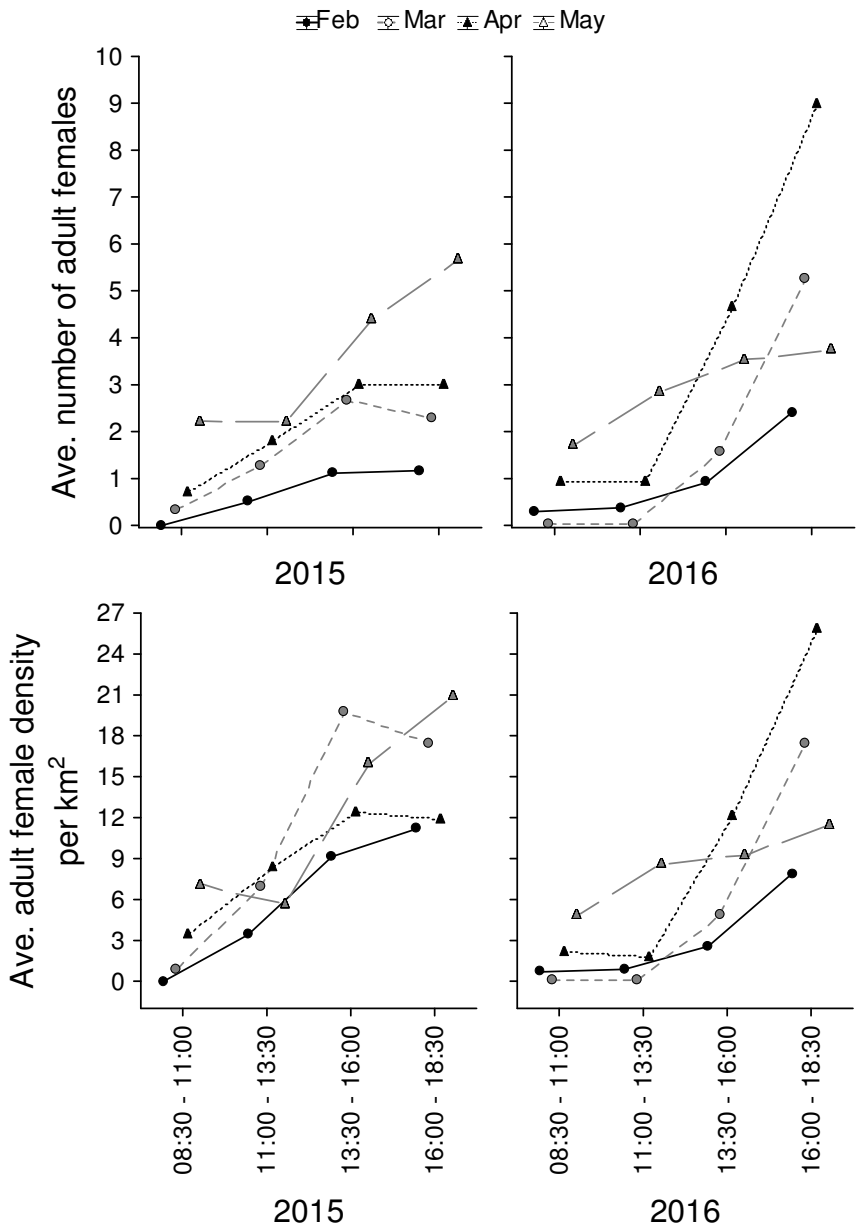
Supplement 4, Figure 1. Grass biomass in the forest habitat of Nagarahole National Park, grassland habitat in Kabini, and forest/savannah-woodland habitat of Bandipur National Park. The values shown are the mean and SD of monthly values (*N*=2 months for Nagarahole forest, 4 months for Kabini grassland, and 5 months for Bandipur forest).

Supplement 4, Table 1. Results from the GLM showing the effects of year (random effect) and month and zones (both fixed effects), and their interactions on grass cover (%). Significant (<0.05) *P* values and effect sizes above 0.2 are marked in bold.

Effect (Fixed/Random)	SS	df_1	MS (effect)	df_2	MS (denom.)	*F*	*P*	Effect size (η^2)
Intercept	1538958.626	1	1538958.626	1	548.326	2806.648	**0.012**	
Year (R)	548.326	1	548.326	144	49.729	11.026	**0.001**	0.027
Month (F)	992.995	3	330.998	3	1495.422	0.221	0.876	0.048
Zone (F)	3153.179	5	630.636	5	104.917	6.011	**0.036**	0.154
Month x Year (R)	4486.267	3	1495.422	144	49.729	30.071	**<.001**	**0.219**
Zone x Year (R)	524.584	5	104.917	144	49.729	2.110	0.068	0.026
Month x Zone (F)	1913.959	15	127.597	15	114.153	1.118	0.416	0.093
Zone x Month x Year (R)	1712.291	15	114.153	144	49.729	2.295	**0.006**	0.084
Error	7160.997	144	49.729					**0.349**
Corrected Total SS	20493							

Supplement 4, Table 2. Results from GLM showing the effects of year (random effect) and month and zones (both fixed effects), and their interactions on grass height (cm). Significant (<0.05) *P* values and effect sizes above 0.2 are marked in bold.

Effect (Fixed/Random)	SS	df_1	MS (effect)	df_2	MS (denom.)	*F*	*P*	Effect size (η^2)
Intercept	5351.984	1	5351.984	1	81.090	66.001	0.078	
Year (R)	81.090	1	81.090	144	1.386	58.513	**<0.001**	0.087
Month (F)	48.443	3	16.148	3	21.540	0.750	0.591	0.052
Zone (F)	439.624	5	87.925	5	4.855	18.109	**0.003**	**0.471**
Month x Year (R)	64.621	3	21.540	144	1.386	15.543	**<0.001**	0.069
Zone x Year (R)	24.276	5	4.855	144	1.386	3.504	**0.005**	0.026
Month x Zone (F)	31.778	15	2.119	15	2.946	0.719	0.735	0.034
Zone x Month x Year (R)	44.195	15	2.946	144	1.386	2.126	**0.012**	0.047
Error	199.560	144	1.386					**0.214**
Corrected Total SS	934							



Supplement 4, Figure 2. Temporal profile showing count and density (accounts for area of the focal zone) of unique adult females in the focal zones during 2.5-hour intervals within a sampling day for different months. Each data point is the average obtained from six focal zones sampled on three sampling days in each month in 2015 and four sampling days in each month in 2016. The elephant density around the Kabini backwaters is higher than that reported (less than 2 elephants/km^2) in forests in Nagarahole and Bandipur National Parks (Baskaran and Sukumar 2011).

References

1. Devidas S (1995). *Dynamics of the Herbaceous Layer in a Dry Deciduous Forest of South India (Bandipur National Park)*. Ph.D. thesis, Pondicherry University, Pondicherry, India.
2. Baskaran N and Sukumar R (2011). *Karnataka Elephant Census 2010*. Asian Nature Conservation Foundation and Centre for Ecological Sciences, Indian Institute of Science Technical report to the Karnataka Forest Department, Bangalore, India.

Supplement 5. Homogeneity of slopes test for effect of competitor number on rate of individual-level agonism between and within clans.

Supplement 5, Table 1. Results from homogeneity of slopes test to examine the slopes of the relationship between rate of individual-level agonism and number of female competitors (group size for within-clan agonism and sum of group size for between-clan agonism) during between- and within-clan agonism. Significant *P* values are marked in bold. Whole model statistics: *Multiple* R^2=0.208, $F_{3, 231}$=20.196, P<0.001.

Effect	SS	*df*	MS	*F*	*P*
Intercept	12.850	1	12.850	7.060	0.008
Type of agonism (between-clan/ within-clan)	0.041	1	0.041	0.023	0.881
Number of females	40.257	1	40.257	22.116	**<0.001**
Type of agonism x Number of females	13.898	1	13.898	7.635	**0.006**
Error	420.481	231	1.820		

Supplement 6. Top best-subset models from linear mixed-model analyses of rates of agonism and partitioning of variances in the models explaining the duration of clan-level between-clan encounters.

Supplement 6, Table 1. Top best-subset fixed-effects models explaining the rate of within-clan individual-level agonism per female. Since random effects resulted in singularity due to negligible variance explained by them, mixed effects models were not explored further. Code descriptions are provided at the end. Estimates are provided for variables that feature in each best-subset model, followed by AIC and other statistics of the model

Model no.	Intercept	biomass_ plot	cover_ plot	CV_ biomass_ plot	CV_cover _plot	CV_ height_ plot	height_ plot	month	no._AF	zone	AIC	BIC	df	logLik	AICc	delta	weight
417	-0.035	-	-	-	-	-	0.134	-	0.106	+	533.505	561.936	9	-257.752	534.602	0.000	0.051
133	1.107	-	-	-0.015	-	-	-	-	0.100	-	534.799	547.435	4	-263.399	535.035	0.433	0.041
418	-0.233	0.001	-	-	-	-	0.094	-	0.112	+	534.368	565.959	10	-257.184	535.718	1.115	0.029
386	-0.053	0.001	-	-	-	-	-	-	0.112	+	534.632	563.063	9	-258.316	535.730	1.127	0.029
419	-1.044	-	0.012	-	-	-	0.117	-	0.110	+	534.584	566.175	10	-257.292	535.934	1.331	0.026
129	0.746	-	-	-	-	-	-	-	0.095	-	535.838	545.315	3	-264.919	535.979	1.377	0.025
425	0.094	-	-	-	-0.009	-	0.120	-	0.111	+	534.687	566.278	10	-257.343	536.037	1.434	0.025
421	0.276	-	-	-0.008	-	-	0.115	-	0.107	+	534.730	566.321	10	-257.365	536.080	1.477	0.024
433	-0.065	-	-	-	-	0.000	0.135	-	0.106	+	535.484	567.074	10	-257.742	536.834	2.232	0.017
165	0.936	-	-	-0.013	-	-	0.024	-	0.100	-	536.496	552.292	5	-263.248	536.853	2.251	0.016

Supplement 6, Table 2. Top best-subset fixed-effects models explaining the rate of within-clan individual-level agonism per dyad. Since random effects (year and clan identity) resulted in singularity due to negligible variance explained from them, mixed effects models were not explored further. Estimates are provided for variables that feature in each best-subset model, followed by AIC and other statistics of the model.

Model no.	Intercept	biomass_ plot	cover_ plot	CV_ biomass_ plot	CV_cover _plot	CV_ height_ plot	height_ plot	month	no._AF	zone	AIC	BIC	df	logLik	AICc	delta	weight
386	0.325	0.000	-	-	-	-	-	-	-0.043	+	241.464	269.896	9	-111.732	242.562	0.000	0.047
417	0.362	-	-	-	-	-	0.047	-	-0.046	+	241.675	270.106	9	-111.837	242.772	0.211	0.042
418	0.271	0.000	-	-	-	-	0.028	-	-0.043	+	242.376	273.967	10	-111.188	243.726	1.164	0.026
402	0.231	0.000	-	-	-	0.003	-	-	-0.041	+	242.590	274.181	10	-111.295	243.940	1.378	0.023
390	0.468	0.000	-	-0.003	-	-	-	-	-0.043	+	242.699	274.290	10	-111.350	244.049	1.487	0.022
421	0.506	-	-	-0.004	-	-	0.038	-	-0.045	+	242.787	274.377	10	-111.393	244.136	1.575	0.021
406	0.414	0.000	-	-0.006	-	0.004	-	-	-0.040	+	242.766	277.515	11	-110.383	244.395	1.834	0.019
433	0.291	-	-	-	-	0.002	0.049	-	-0.045	+	243.049	274.639	10	-111.524	244.398	1.837	0.019
389	0.790	-	-	-0.006	-	-	-	-	-0.047	+	243.360	271.792	9	-112.680	244.458	1.896	0.018
425	0.397	-	-	-	-0.002	-	0.043	-	-0.044	+	243.356	274.946	10	-111.678	244.705	2.144	0.016

Supplement 6, Table 3. Top best-subset fixed-effects models explaining the rate of between-clan individual-level agonism per female per hour. Since random effect of year resulted in singularity due to negligible variance explained by year, mixed effects models were not explored further. Estimates are provided for variables that feature in each best-subset model, followed by AIC and other statistics of the model.

Model no.	Intercept	biomass_plot	biomass_zone	cover_plot	cover_zone	CV_biomass_zone	CV_cover_zone	CV_height_zone	diff_AF	height_plot	height_zone	month	sum_AF	zone	AIC	BIC	df	logLik	AICc	delta	Weight
7425	2.906	-	-	-	-	-	-	-	-	-0.408	-	+	0.382	+	206.050	227.723	11	-92.025	212.489	0.000	0.034
7429	8.336	-	-	-0.059	-	-	-	-	-	-0.371	-	+	0.341	+	205.787	229.430	12	-90.893	213.587	1.098	0.019
3073	0.183	-	-	-	-	-	-	-	-	-	-	+	0.355	-	212.294	224.116	6	-100.147	214.120	1.631	0.015
7426	3.783	-0.001	-	-	-	-	-	-	-	-0.368	-	+	0.346	+	206.837	230.480	12	-91.418	214.637	2.148	0.011
3841	-0.359	-	-	-	-	-	-	-	-	-0.441	0.525	+	0.383	-	211.510	227.273	8	-97.755	214.783	2.294	0.011
7553	2.638	-	-	-	-	-	-	-	-0.191	-0.398	-	+	0.501	+	207.152	230.795	12	-91.576	214.952	2.463	0.010
7183	0.053	-	-0.005	-0.135	0.184	-	-	-	-	-	-	+	0.345	+	205.889	231.503	13	-89.944	215.222	2.733	0.009
3074	1.620	-0.002	-	-	-	-	-	-	-	-	-	+	0.304	-	212.834	226.626	7	-99.417	215.323	2.834	0.008
3329	1.315	-	-	-	-	-	-	-	-	-0.187	-	+	0.340	-	212.907	226.699	7	-99.453	215.395	2.906	0.008
7441	3.995	-	-	-	-	-0.049	-	-	-	-0.467	-	+	0.416	+	207.635	231.278	12	-91.817	215.435	2.946	0.008

Supplement 6 Table 4. Top best-subset fixed-effects models explaining the rate of between-clan agonistic encounters per clan per 2.5-hour interval. Since random effect of year resulted in singularity due to negligible variance explained by year, mixed effects models were not explored further. Estimates are provided for variables that feature in each best-subset model, followed by AIC and other statistics of the model.

Model no.	Intercept	area_ zone	clan_ count	month	zone	zone_ biomass	zone_ cover	CV_ biomass _zone	CV_ cover_ zone	CV_ height_ zone	zone_ height	AIC	BIC	df	logLik	AICc	delta	weight
3	-0.826	-	0.461	-	-	-	-	-	-	-	-	193.289	203.333	4	-92.645	193.755	0.000	0.623
4	-0.866	0.139	0.458	-	-	-	-	-	-	-	-	194.781	207.336	5	-92.391	195.487	1.733	0.262
515	-0.686	-	0.460	-	-	-	-	-	-	-	-0.023	199.530	212.084	5	-94.765	200.236	6.481	0.024
7	-0.501	-	0.420	+	-	-	-	-	-	-	-	199.027	216.603	7	-92.514	200.377	6.622	0.023
131	-0.922	-	0.458	-	-	-	-	-	0.016	-	-	200.722	213.276	5	-95.361	201.428	7.673	0.013
516	-0.727	0.155	0.456	-	-	-	-	-	-	-	-0.024	200.993	216.058	6	-94.497	201.993	8.239	0.010
8	-0.517	0.048	0.419	+	-	-	-	-	-	-	-	200.604	220.691	8	-92.302	202.361	8.606	0.008
132	-0.998	0.235	0.453	-	-	-	-	-	0.017	-	-	202.043	217.108	6	-95.022	203.043	9.289	0.006
35	-1.096	-	0.460	-	-	-	0.003	-	-	-	-	202.464	215.018	5	-96.232	203.170	9.415	0.006
67	-0.751	-	0.463	-	-	-	-	-0.004	-	-	-	202.586	215.141	5	-96.293	203.292	9.538	0.005

Supplement 6 Table 5a. Top best-subset fixed-effects models explaining the duration of between-clan agonistic encounters per clan per 2.5-hour interval. Since random effect of year resulted in singularity due to negligible variance explained by year, mixed effects models were not explored further. Estimates are provided for variables that feature in each best-subset model, followed by AIC and other statistics of the model.

Model no.	(Intercept)	biomass_plot	biomass_zone	cover_plot	cover_zone	CV_biomass_zone	CV_cover_zone	CV_height_zone	diff_AF	height_plot	height_zone	sum_AF	AIC	BIC	df	logLik	AICc	delta	weight
6	289.871	0.161	-	-3.813	-	-	-	-	-	-	-	-	493.801	501.369	4	-242.901	494.711	0.000	0.050
38	337.073	0.145	-	-4.031	-	-	-2.338	-	-	-	-	-	493.852	503.311	5	-241.926	495.248	0.537	0.038
70	285.929	0.154	-	-3.646	-	-	-	-0.378	-	-	-	-	495.196	504.655	5	-242.598	496.591	1.881	0.020
22	280.526	0.172	-	-3.954	-	0.675	-	-	-	-	-	-	495.200	504.659	5	-242.600	496.595	1.884	0.020
14	227.728	0.151	-	-4.105	1.044	-	-	-	-	-	-	-	495.421	504.880	5	-242.710	496.816	2.106	0.017
54	329.991	0.158	-	-4.235	-	0.870	-2.583	-	-	-	-	-	494.832	506.183	6	-241.416	496.832	2.121	0.017
262	311.867	0.174	-	-4.031	-	-	-	-	-	-1.925	-	-	495.526	504.985	5	-242.763	496.921	2.210	0.017
8	269.919	0.146	0.017	-3.607	-	-	-	-	-	-	-	-	495.627	505.086	5	-242.814	497.023	2.312	0.016
518	274.281	0.153	-	-3.687	-	-	-	-	-	-	1.692	-	495.649	505.108	5	-242.825	497.045	2.334	0.016
1030	273.112	0.156	-	-3.618	-	-	-	-	-	-	-	0.382	495.675	505.134	5	-242.838	497.071	2.360	0.015

Supplement 6, Table 5b. Partitioning of variances for the fixed effects of within-plot-cluster biomass and cover on duration of between-clan agonistic encounters. The effect size (η^2) was calculated from the ANOVA table which was obtained after running the function *anova()* in R.

Effect	SS	*df*	MS (effect)	*F*	*P*	η^2
Within-plot-cluster biomass	25067	1	25066.6	19.879	**<0.001**	0.300
Within-plot-cluster cover	547	1	547.1	0.4339	0.513	0.007
Residuals	58003	46	1260.9	-	-	0.694

Code descriptions:

zone: focal zone (n=6) of sampling, month: month (n=4) of sampling, year: year (n=2) of sampling, clan_id: name of clan of the group on which focal group observation was taken.

biomass_plot: within-plot grass biomass; cover_plot: within-plot grass cover; height_plot: within-plot grass height;

CV_biomass_plot: within plot-cluster coefficient of variation in grass biomass; CV_biomass_cover: within plot-cluster coefficient of variation in grass cover; CV_biomass_height: within plot-cluster coefficient of variation in grass height;

no._AF: number of adult females in the group; sum_AF: total number of adult females (group size in the case of within-clan agonism and sum of group sizes in the case of between-clan agonism); diff_AF: absolute difference in adult female group sizes of the two competing groups; zone_area: area of the focal zone in the month of sampling;

cover_zone: within-zone average grass cover; biomass_zone: within-zone average grass biomass; height_zone: within-zone average grass height;

CV_cover_zone: within-zone coefficient of variation in average grass cover; CV_biomass_zone: within-zone coefficient of variation in average grass biomass; CV_height_zone: within-zone coefficient of variation in average grass height.

Supplement 7. Best-subset model of within-clan agonism, and scatter-plots of the relationships between ecological variables (grass abundance, distribution, and number of competitors) and within-clan and individual-level between-clan agonism.

Results from the best-subset model explaining within-clan rate of individual-level agonism per female had been shown in the main text. The results from the best-subset model for within-clan rate of inter-individual agonism per dyad is shown in the table below. Scatterplots showing how within-clan agonism, individual-level between-clan agonism, and duration of clan-level between-clan agonism vary with the independent variables explored, i.e. grass biomass, cover, and height, CV in grass biomass, cover, and height, group size (for within-clan agonism), sum of group size, difference in group size (for between-clan individual-level agonism), and number of clans, are shown in figures below.

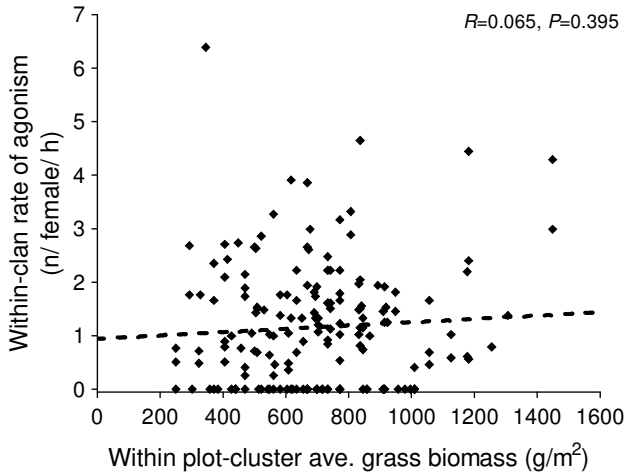
Supplement 7, Table 1. Results from the best-subset fixed effects model explaining dyadic rate (per female dyad per hour) of within-clan agonism.

Fixed/ Random	Effect	Estimate	S.E. of estimate	95% CI of estimate		*t*	*P*
	Intercept	0.325	0.177	-0.021	0.670	1.833	0.069
Fixed	Group size	-0.043	0.017	-0.076	-0.009	-2.501	0.013
Fixed	Within-plot-cluster biomass	0.000	0.000	0.000	0.001	-2.167	0.032
Fixed/ Random	Effect	Estimate	S.E. of estimate	95% CI of estimate		*t*	*P*

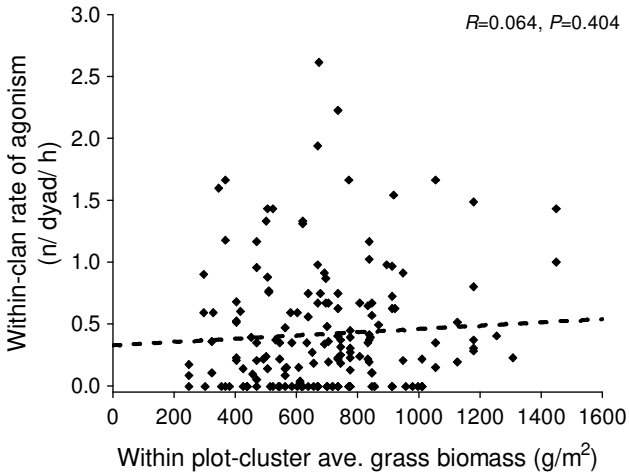
Fixed	Zone- KKU	0.285	0.158	-0.024	0.593	1.798	0.074
Fixed	Zone- MK	-0.292	0.129	-0.544	-0.040	-2.257	0.025
Fixed	Zone- NB	-0.138	0.143	-0.417	0.141	-0.963	0.337
Fixed	Zone- RKB	0.045	0.096	-0.142	0.231	0.465	0.642
Fixed	Zone- TH	0.196	0.128	-0.053	0.446	1.537	0.126
	Multiple R^2	0.128					

Within-clan rate of individual-level agonism per female per hour	Within-clan rate of individual-level agonism per dyad per hour

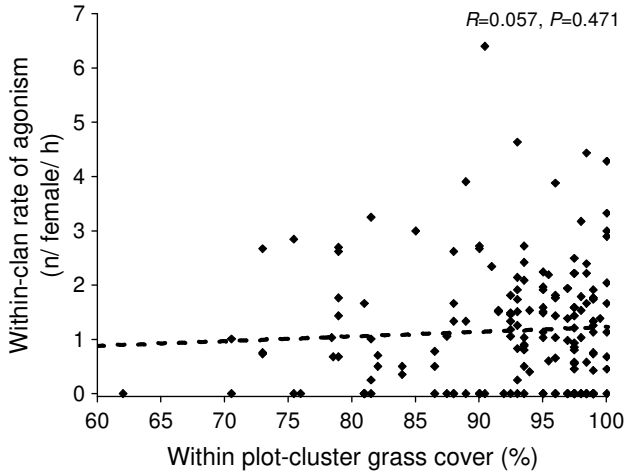
a)



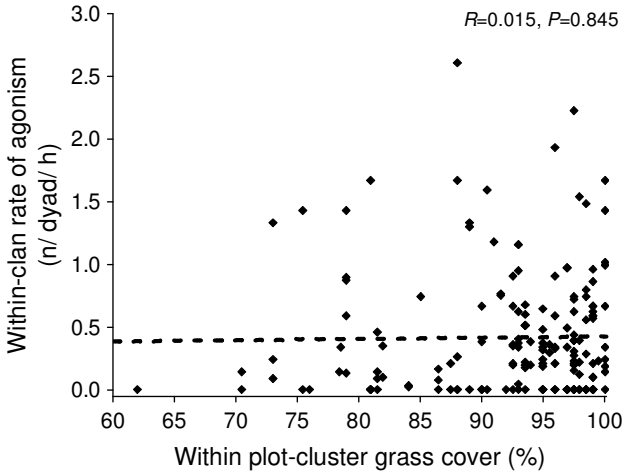
b)



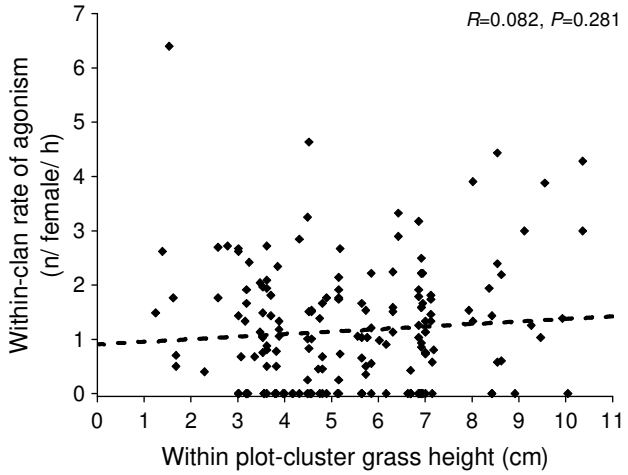
c)



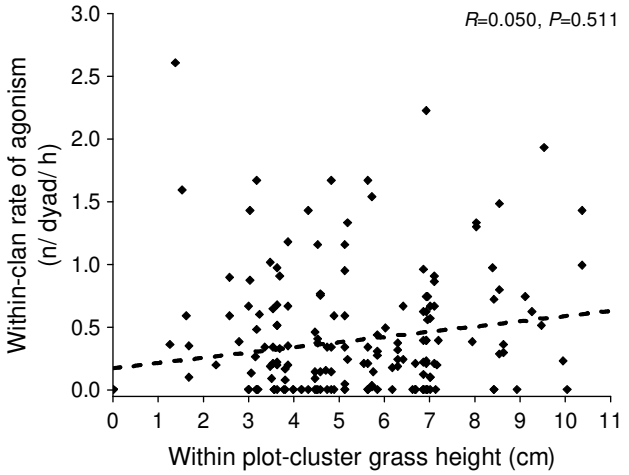
d)

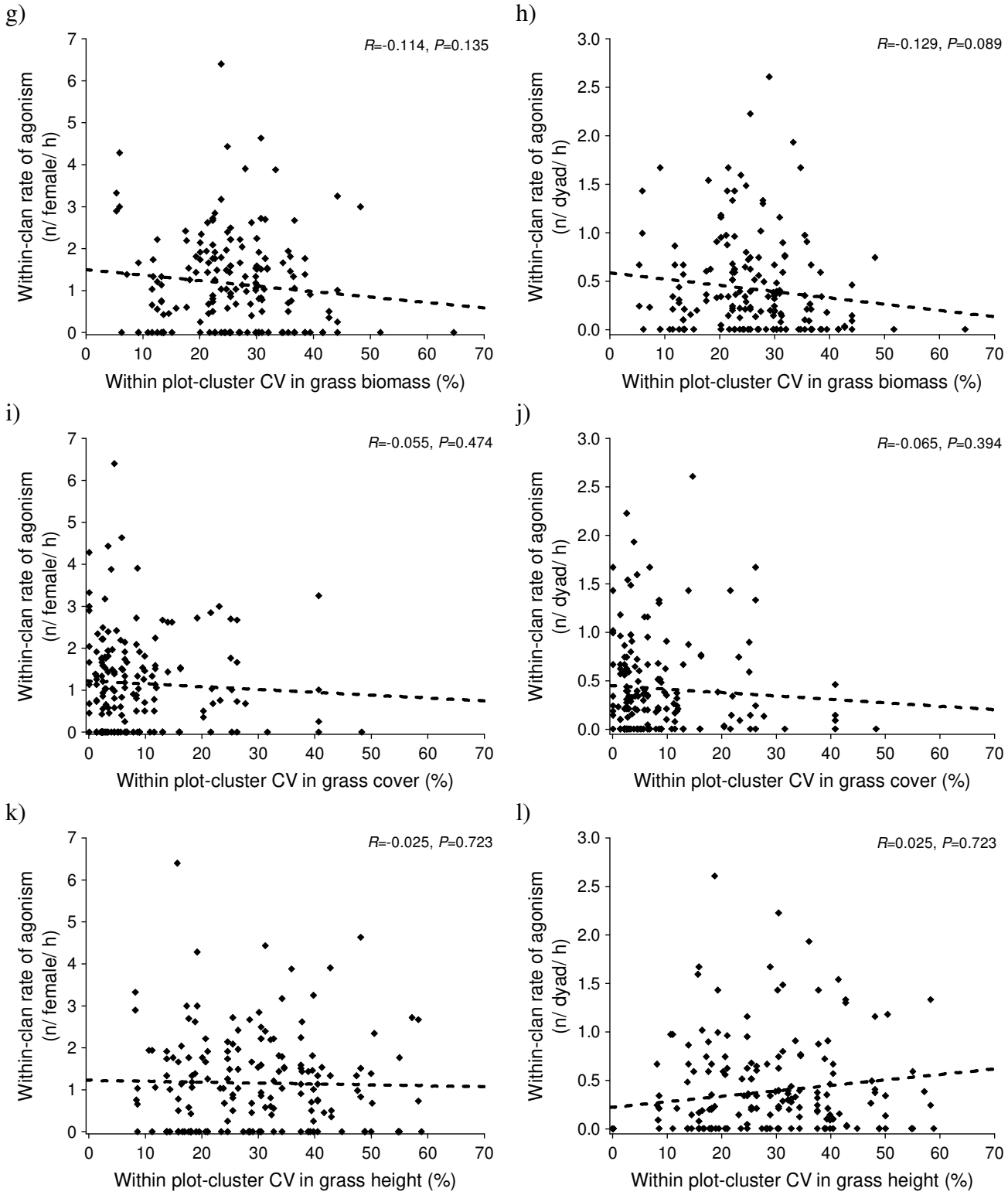


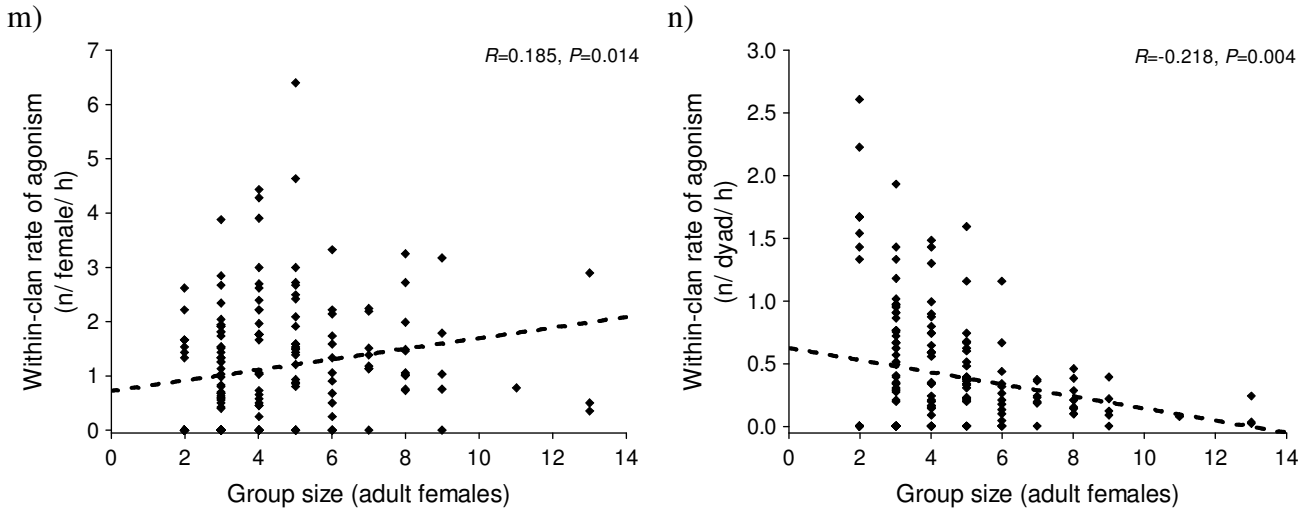
e)



f)

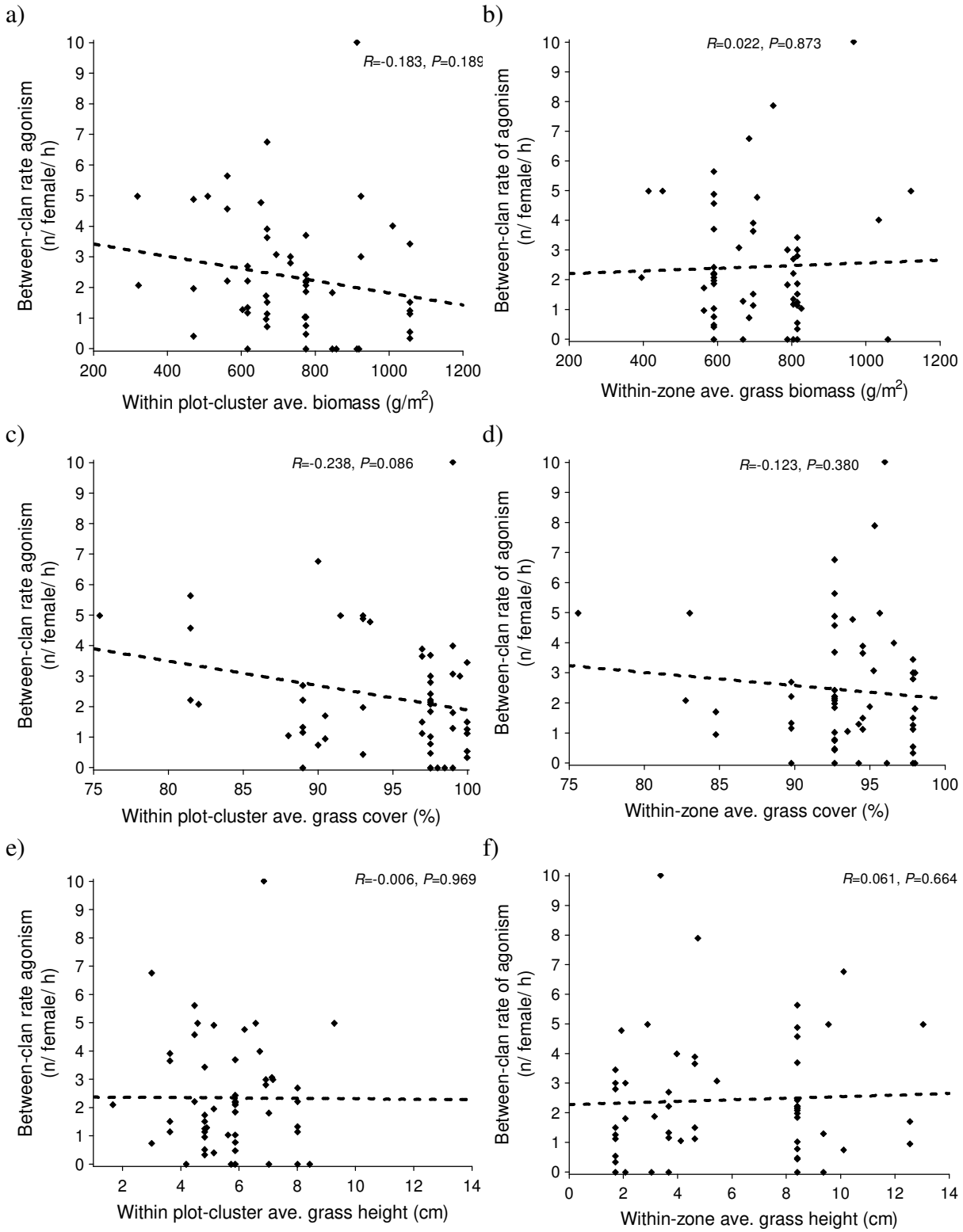


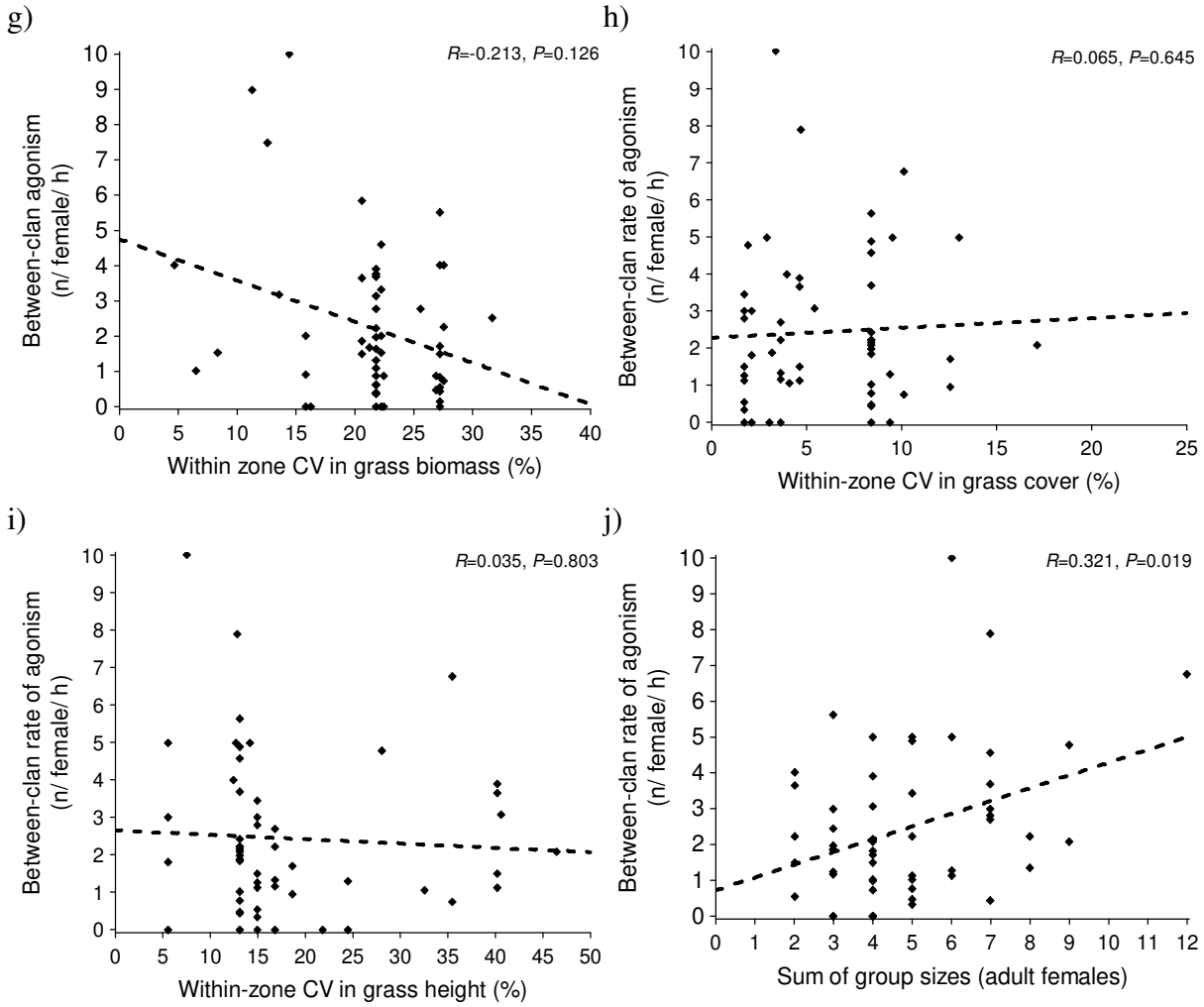

g)
R=-0.114, P=0.135
Within-clan rate of agonism (n/ female/ h)
Within plot-cluster CV in grass biomass (%)
h)
R=-0.129, P=0.089
Within-clan rate of agonism (n/ dyad/ h)
Within plot-cluster CV in grass biomass (%)
i)
R=-0.055, P=0.474
Within-clan rate of agonism (n/ female/ h)
Within plot-cluster CV in grass cover (%)
j)
R=-0.065, P=0.394
Within-clan rate of agonism (n/ dyad/ h)
Within plot-cluster CV in grass cover (%)
k)
R=-0.025, P=0.723
Within-clan rate of agonism (n/ female/ h)
Within plot-cluster CV in grass height (%)
l)
R=0.025, P=0.723
Within-clan rate of agonism (n/ dyad/ h)
Within plot-cluster CV in grass height (%)



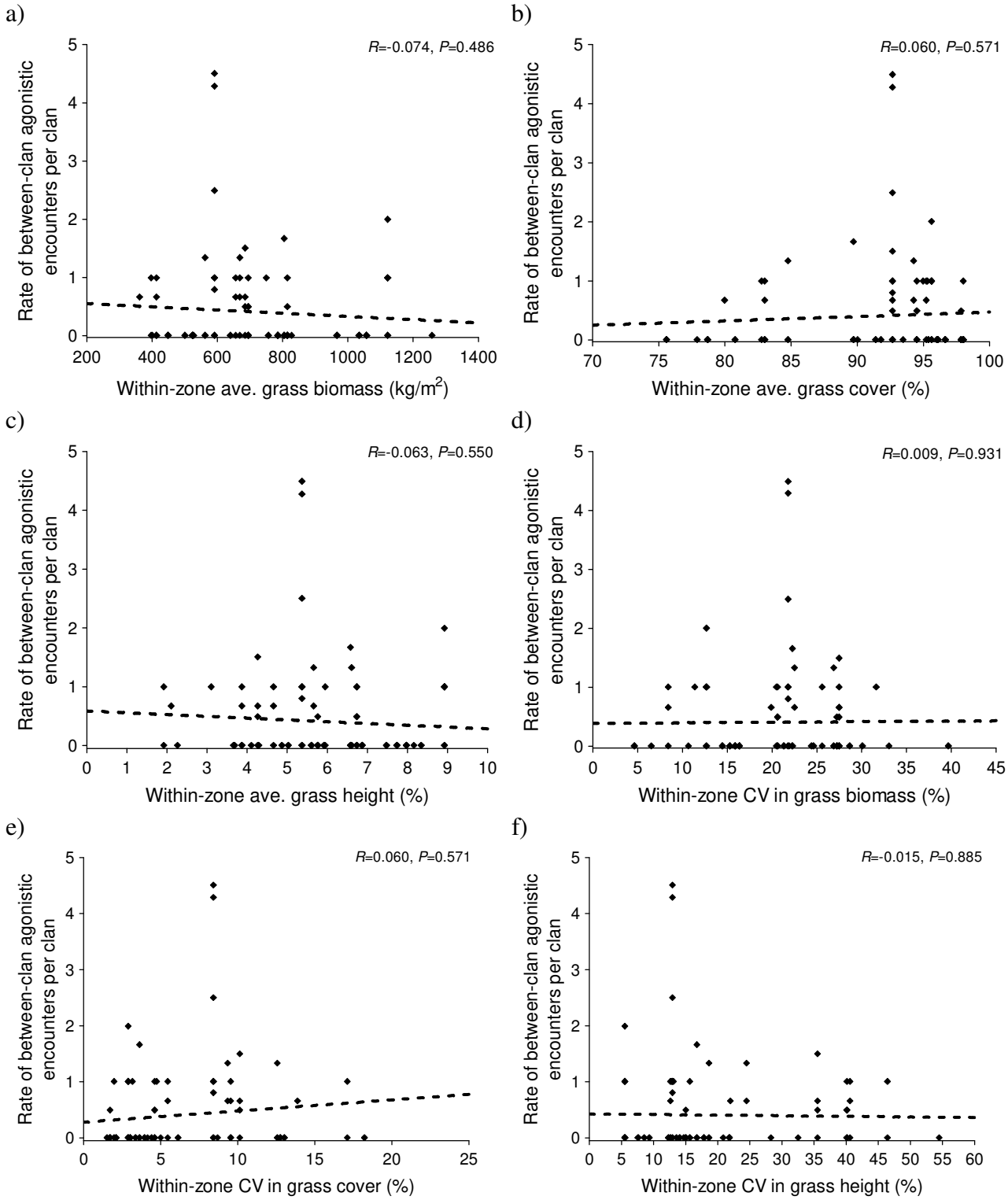
Supplement 7, Figure 1. Scatterplots showing the relationship between within-clan agonism and grass abundance (biomass, grass cover, and grass height), CV in grass abundance, and group size.

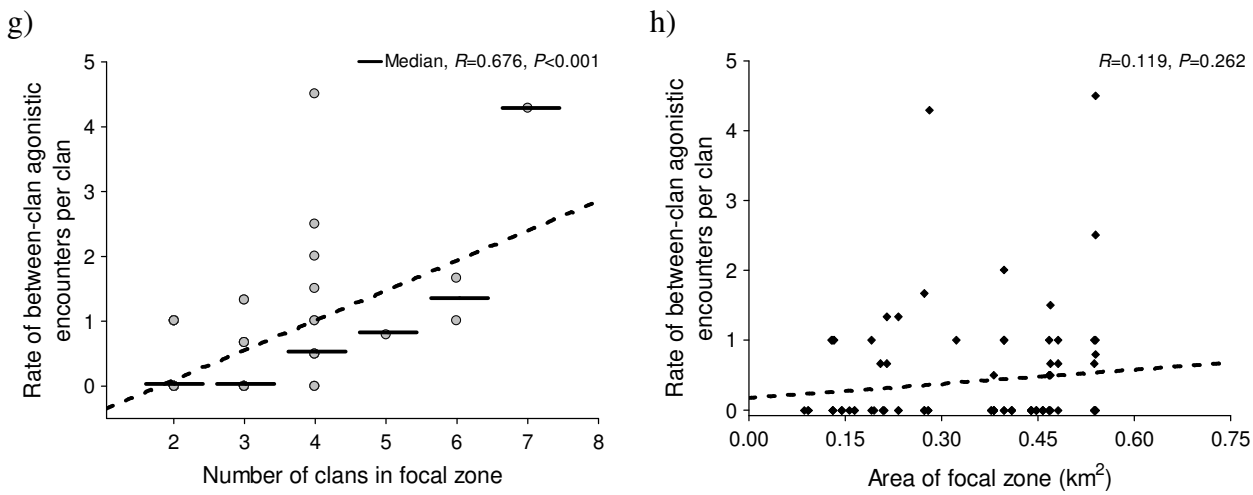
1


a)
R=-0.183, P=0.189
Between-clan rate agonism (n/ female/ h)
Within plot-cluster ave. biomass (g/m2)
b)
R=0.022, P=0.873
Between-clan rate of agonism (n/ female/ h)
Within-zone ave. grass biomass (g/m2)
c)
R=-0.238, P=0.086
Between-clan rate agonism (n/ female/ h)
Within plot-cluster ave. grass cover (%)
d)
R=-0.123, P=0.380
Between-clan rate of agonism (n/ female/ h)
Within-zone ave. grass cover (%)
e)
R=-0.006, P=0.969
Between-clan rate agonism (n/ female/ h)
Within plot-cluster ave. grass height (cm)
f)
R=0.061, P=0.664
Between-clan rate of agonism (n/ female/ h)
Within-zone ave. grass height (cm)

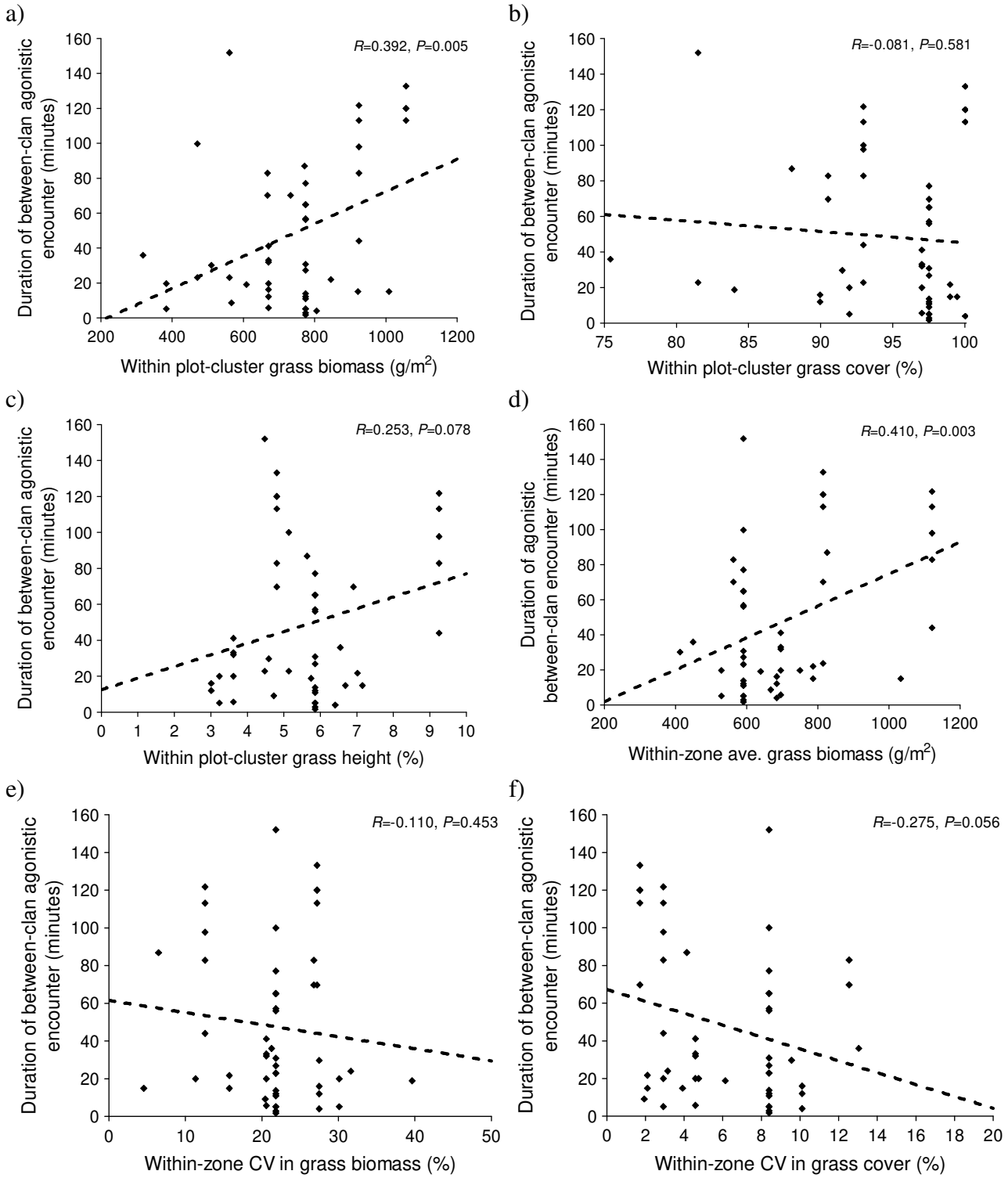


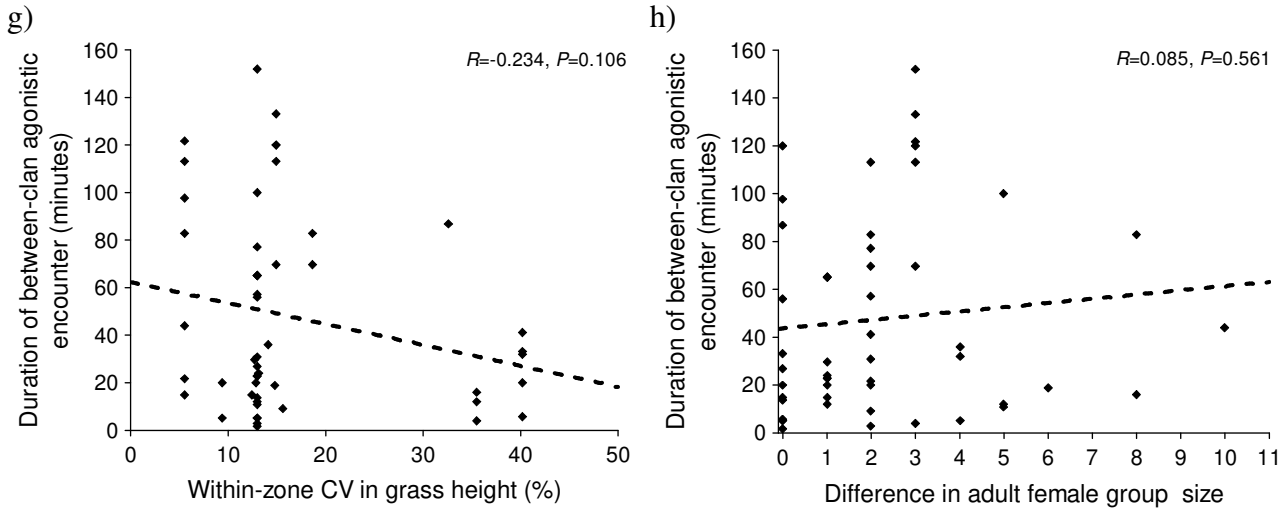
Supplement 7, Figure 2. Scatterplots showing how the rate of individual-level between-clan agonism is related to grass abundance, grass distribution, average group size, and sum of group sizes of the contestant groups. Some data points in panel j mask others due to overlap.


a)
R=-0.074, P=0.486
Rate of between-clan agonistic encounters per clan
Within-zone ave. grass biomass (kg/m2)
b)
R=0.060, P=0.571
Rate of between-clan agonistic encounters per clan
Within-zone ave. grass cover (%)
c)
R=-0.063, P=0.550
Rate of between-clan agonistic encounters per clan
Within-zone ave. grass height (%)
d)
R=0.009, P=0.931
Rate of between-clan agonistic encounters per clan
Within-zone CV in grass biomass (%)
e)
R=0.060, P=0.571
Rate of between-clan agonistic encounters per clan
Within-zone CV in grass cover (%)
f)
R=-0.015, P=0.885
Rate of between-clan agonistic encounters per clan
Within-zone CV in grass height (%)



Supplement 7, Figure 3. Scatterplots showing how the rate of (clan-level) between-clan agonistic encounters per clan per 2.5-hour interval varies with grass abundance (biomass, cover, height), grass distribution (CV in grass biomass, cover, and height), number of clans in focal zones, and area of the focal zone. Each data point is a 2.5-hour interval during which two or more clans were present in the focal zone. In g), since data points may be masked due to overlap, medians are also plotted against each value of the number of clans.


a)
R=0.392, P=0.005
Duration of between-clan agonistic encounter (minutes)
Within plot-cluster grass biomass (g/m2)
b)
R=-0.081, P=0.581
Duration of between-clan agonistic encounter (minutes)
Within plot-cluster grass cover (%)
c)
R=0.253, P=0.078
Duration of between-clan agonistic encounter (minutes)
Within plot-cluster grass height (%)
d)
R=0.410, P=0.003
Duration of agonistic between-clan encounter (minutes)
Within-zone ave. grass biomass (g/m2)
e)
R=-0.110, P=0.453
Duration of between-clan agonistic encounter (minutes)
Within-zone CV in grass biomass (%)
f)
R=-0.275, P=0.056
Duration of between-clan agonistic encounter (minutes)
Within-zone CV in grass cover (%)



Supplement 7, Figure 4. Scatterplots showing how the duration of clan-level between-clan agonistic encounters varies with within plot-cluster and within-zone grass abundance (biomass, cover, and height), within-zone grass distribution (CV in grass biomass, cover, and height), and difference in group sizes of the competing clans.