Welfare of captive breeding stock for reintroductions into Saudi Arabian National Parks: assessment of aggressiveness and dominance hierarchies in true gazelles (*Gazella* spp.) using social network analysis

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Running title: Social network analysis in *Gazella* captive breeding stock

ABSTRACT

Populations of true gazelles [*Gazella arabica*, *G. dorcas* ('*G. saudiya*') and *G. marica*] on the Arabian Peninsula have suffered dramatically from hunting and poaching, habitat degradation, and competition with livestock. Several captive breeding facilities are devoted to the conservation of those taxa, and captive breeding stock is regularly used for reintroductions into National Parks, or for the restocking of declining populations. A prerequisite for successful reintroductions, however, is a natural behavioral repertoire of individuals identified for reintroduction campaigns. This highlights the need for behavioral studies in captive breeding groups to (*a*) identify potential aberrant behavior and (*b*) to test if breeding conditions bring about increased stress levels due to abnormally high aggressiveness. In this study, we exemplify the utility of social network analysis for the investigation of aggressiveness and social dominance hierarchies in different breeding groups of gazelles at the King Khalid Wildlife Research Center. At the same time, we tested several *a priori* hypotheses on the potential role of female horns in predicting their network position, as female horn development varies dramatically not only between different taxa but also within breeding groups. For example, the ‘female competition hypothesis’ assumes bovid females to use their horns in competition with other female group members, while the ‘andromimicry hypothesis’ assumes horned females to mimic the male phenotype, thereby raising the threshold for male aggression against adolescent male offspring and enabling their male offspring to leave the group at a later stage. We built reciprocated, weighted networks from socio-positive and socio-negative interactions between female group members. Tests of the ‘female competition hypothesis’ assumed horn length to predict individuals’ network position. Several network parameters calculated from socio-negative behaviors were predicted to correlate with inter-individual variation in horn length within, or variation in mean horn length between groups, but no such pattern was uncovered. However, we found support for predictions derived from the ‘andromimicry hypothesis’ in that network parameters calculated from socio-positive behaviors (network strength and reciprocated network strength) decreased with increasing mean (group-level) horn length. Females could mimic the phenotype of their juvenile male offspring not only morphologically (by developing horns), but also on a behavioral level, leading to male-like behavior and including reduced socio-positive behavior. Our study demonstrates pronounced behavioral variation in overall aggressiveness and dominance stratifications among the examined groups of gazelles, with no indication for any obvious shift towards an aberrant form of dominance stratification (like extremely biased and continued socio-negative behavior being directed at few subordinate individuals). Levels of aggressiveness appeared to range well within those found in natural populations, altogether highlighting the suitability of stock from this particular breeding facility for the restocking of National Parks.

Keywords: re-introduction, directed networks, secondary sexual characters, andromimicry, weighted networks

INTRODUCTION

Conservation of Arabian gazelles

Gazelles were once amongst the most frequently encountered wildlife species in Arabian deserts

(Vesey-Fitzgerald, 1952; Philby, 1957; Thesiger, 1959). Three species, namely, the sand gazelle (*Gazella marica*), the Arabian gazelle (*Gazella arabica*; until recently thought to be synonymous to its ecologically and behaviorally similar sister species, the mountain gazelle, *Gazella gazella*; Wronski et al., 2010b; Bärmann et al., 2013) and the Saudi gazelle (*Gazella saudiya*; the Arabian subspecies of dorcas gazelle, *Gazella dorcas*; Hammond et al., 2001; Lerp et al., 2011), occupied most of the major habitat types on the Arabian Peninsula. Gazelles were found from the humid parklands along the Red Sea shoreline to the high basalt plateaus and lava fields of the north, but also in the undulating gravel plains and huge dune systems of the center and along the shores of the Arabian Gulf in the east (Habibi & Williamson, 1997). Within living memory, gazelles were sufficiently numerous in Saudi Arabia, sometimes seen in very large numbers. In recent times, however, they have disappeared from most of their former range (Child & Grainger, 1990; Thouless et al., 1991; Dunham et al., 2001; Cunningham & Wacher, 2009). Apart from the Farasan Islands in the Red Sea (Cunningham & Wronski, 2011a; Wronski, 2013), small parts of basaltic desert in the central north, and isolated pockets in the more inaccessible valleys of the western mountains (Seddon et al., 1997; Boug et al., 2013) gazelles are entirely extirpated.

The rapid decline of gazelles from nearly all of their former range within a period of only 60 years became a source of major concern in Saudi Arabia. To counteract this development, the government of Saudi Arabia founded the National Commission for Wildlife Conservation and Development (now Saudi Wildlife Authority, SWA) in 1986 and established several protected areas and reserves in the Kingdom (Child & Grainger, 1991). This system of protected areas was intended to act as a refuge for wildlife in general and together with captive breeding and reintroduction programs supposed to serve as a conservation tool for the restoration of the three gazelle species in Saudi Arabia. Several reintroduction and restocking initiatives were more or less successfully implemented in Saudi Arabia. These include the release of Arabian gazelles into the Ibex Reserve and the Uruq Bani Ma'arid National Park (Wronski et al., 2012; Islam et al., 2012), the release of sand gazelles into Uruq Bani Ma'arid National Park (Wacher & Kichenside, 1998) and the introduction of Arabian and sand gazelles into Mahazat as-Sayd Protected Area (Haque & Smith, 1996; Islam et al., 2014).

Soon after the establishment of the SWA, two captive breeding centers were established; the National Wildlife Research Centre (NWRC) near Taif, specializing primarily in captive breeding and reintroduction of Arabian oryx (*Oryx leucoryx*), and the King Khalid Wildlife Research Centre (KKWRC) at Thumamah near Riyadh, which concentrates on gazelle breeding and reintroduction. The establishment and development of the captive breeding centers has run concurrent with the development of protected areas, so that in several cases gazelles bred in captivity became available for reintroductions simultaneously, or only shortly after, the legal declaration of newly protected areas. Key objectives for gazelle reintroductions are to restore genetically, clinically and behaviorally healthy wild populations, which ideally become self-sustaining, within their natural historic range at locations where the original reasons for extinction are identified and no longer prevail.

In this context, several questions arise regarding the behavior and social organization of gazelles held, e.g., at KKWRC. Suboptimal rearing conditions can lead to increased levels of aggressive behaviors amongst the members of captive breeding groups (Calhoun, 1962; Christian, 1963; Morgan & Tromborg, 2007), and our present study provides first insights into this potential problem by investigating aggressive interactions among the members of female breeding groups of different species of gazelles. Likewise, we asked if captive breeding groups of gazelles would show abnormally structured dominance hierarchies, where insufficient space leads to unusually high levels of aggressive behavior being directed at subordinate individuals (Peel et al., 2005; Morgan & Tromborg, 2007).

Female horns, aggressiveness, and social network position

We coupled our analysis of aggressive behavior and social network structures in female breeding groups of *Gazella* spp. with the question of whether and how inter- and intraspecific variation in female horn length might affect the occurrence of aggressive behaviors in female groups and the structure of dominance hierarchies. Uneven-toed ungulates show an amazing degree of variation in the expression of secondary sexual characters, which has inspired a wealth of studies trying to explain the evolution of antlers, horns, elongated canines and other traits in the male sex (Geist, 1966; Prothero & Schoch, 2002; Caro et al., 2003). For example, giant antlers in extinct *Megaloceros giganteus* deer stimulated hypotheses on the coevolution of female mating preferences and sexually selected male traits (inter-sexual selection; Fisher, 1930; Miller, 2000; Kokko & Brooks, 2003; Bonduriansky, 2007). Also, the use of male weaponry in mate competition (intra-sexual selection) is well documented (e.g., Clutton-Brock, 1982; Clutton-Brock, et al., 1982; Lundrigan, 1996; Pelletier et al., 2006; Vanpé et al., 2007; Plard et al., 2011). Recent studies have started to investigate the effects of human hunting pressure and environmental deterioration on the expression of these traits (e.g., Hedrick, 2011).

An often overlooked phenomenon in this group, however, is the expression of secondary sexual characters in females. For example, females of most species of deer (Cervidae) have no antlers, while caribou (*Rangifer tarandus*) females possess well-developed antlers (Schaefer & Mahoney, 2001). Variation in female weaponry is prominent within the family of horned ungulates (Bovidae; Kiltie, 1985), such as the spiral-horned antelopes (genus *Tragelaphus*), in which only bongo (*T. euryceros*), common (*T. oryx*), and giant eland (*T. derbianus*) females possess horns, while females are hornless in the other six members of this group (Kingdon, 2013). Other clades of the bovid family show more continuous variation in the development of female horns. For example, females of eight species of true gazelles (genus *Gazella*) possess horns, and only goitered gazelle (*G. subgutturosa*) females are hornless [Kingswood & Blank (1996); goitered gazelles were considered to be synonymous to sand gazelles, *G. marica*—whose females possess horns—prior to the phylogenetic analysis by Wacher et al. (2011), leading to a misclassification, e.g., in Stankowich & Caro (2009)]. Considerable variation is seen in the length and shape of adult females' horns in the former eight taxa (Wronski et al., 2010a), ranging from minute (or sometimes absent) horns in female Arabian gazelles on the Farasan Islands (described as '*Gazella arabica farasani*'; Thouless & Al Basri, 1991; but see Lerp et al., 2014) to species in which females show well-developed horns, as seen in slender-horned gazelles (*G. leptoceros*; Beudels & Devillers, 2013).

Four hypotheses seek to explain the presence or absence of horns in female bovids: (1) According to the 'predator defense hypothesis' female horns evolved as a means of defense against predator attacks (Darling, 1937; Packer, 1983; Stankowich & Caro, 2009). (2) The 'intra-specific competition hypothesis' assumes that females use horns during feeding competition with males or to avoid male sexual harassment (Geist, 1974a, b, 1977; Janis, 1982). (3) Females may use their horns in competition with other female group members ('female competition hypothesis'; Roberts, 1996). (4) Finally, the 'andromimicry hypothesis' suggests that females could mimic the phenotype of their juvenile male offspring, thereby raising the threshold for male aggression against adolescent male offspring and enabling their male offspring to leave the group at a later stage (Estes, 1991, 2000, 2011). Behavioral experiments to test those hypotheses are as yet lacking, and empirical support, e.g., for the potential function of female horns for predator defense (hypothesis 1) is restricted to *in situ* observations (Caro et al., 2004). Stankowich & Caro (2009) used a phylogenetic approach and indirectly inferred that the primary function of horns in bovid females could be linked to anti-predator defense in most clades, but occasionally to intra-sexual competition in others. Likewise, testing whether females use their horns for defense from male sexual harassment (hypothesis 2) is restricted to observations during the mating season and was not feasible in the course of our present study.

Our study was not designed to contrast and evaluate the validity of all four hypotheses, and we acknowledge that they may not necessarily be mutually exclusive. However, hypotheses (3)—the 'female competition hypothesis'—and (4)—the 'andromimicry hypothesis'—offer a set of testable predictions on which our present study builds. We tested predictions derived from those hypotheses using social network analysis of artificially composed female groups held at KKWRC, which showed variation in horn length not only within groups (partly reflecting age-effects; Wronski et al., 2010a), but also considerable variation among different breeding groups (Figure 1).

FIGURE 1

Mutual interactions among the members of animal societies can be used to build social networks and to analyze various parameters characterizing individuals' network position, a technique that is increasingly used in behavioral ecology (Croft et al., 2008; Whitehead, 2008; Krause et al., 2014). Especially social networks built from directed and weighted behavioral measures provide a powerful, novel tool (see Squartini et al., 2013 for a methodological description). In our present study, we thus not only calculated classic dominance indices, but also built social networks from socio-negative and socio-positive interactions among females in captive groups of gazelles. We tested the following predictions derived from hypothesis (3)—the 'female competition hypothesis': (*a*) inter-individual variation in horn length could affect an individuals' social status within a group if those individuals that carry longer horns also have a greater resource-holding potential (*sensu* Parker, 1974). Hence, individuals with longer horns should be more dominant, as reflected, e.g., by a lower socio-negative in-strength, a higher socio-negative out-strength, and a lower reciprocated network strength. (*b*) Likewise, dominance indices (Eden, 1987; Clutton-Brock et al., 1979) should increase with increasing individual horn-length. (*c*) Major differences in social organization between different species of gazelles could coincide with taxon-specific differences in female horn development. Taxa with longer horns could be more aggressive overall, which should be reflected by a higher mean (group-level) socio-negative network strength. (*d*) Likewise, stronger dominance stratifications could lead to decreasing reciprocated network strength with increasing mean horn length for both socio-negative and socio-positive behaviors, and (*e*) more linear dominance stratifications could be reflected by higher values of Landau's (1951) index of linearity.

Further predictions can be derived from hypothesis (4)—the 'andromimicry hypothesis': If females indeed mimic males in morphology and behavior to reduce male aggression towards adolescent male offspring [i.e., because breeding males treat young males as potential rivals once their horns become conspicuous and drive them from female herds and territories (Estes, 1991, 2000, 2011)], the following differences between groups are to be expected: groups with longer horns should show more "male-like" behavior, i.e., they should show (f) increased aggression overall [congruent with prediction (c), see above], and (g) reduced socio-positive behavior, as territorial males uniformly respond aggressively, but not socio-positively, to other males. This should be reflected by a decreasing mean (group-level) socio-positive network strength and decreasing reciprocated socio-positive network strength with increasing mean (group-level) horn length.

MATERIAL AND METHODS

Study area and animals

Behavioral observations were carried out at King Khalid Wildlife Research Center (KKWRC) in central Saudi Arabia. The captive breeding scheme at KKWRC consists of some 60 rectangular pens each measuring app. 100 × 50 m. A double fence separates the enclosures to prevent nose-to-nose contact between adjacent groups. Draping fences between pens with shade netting reduce visual contact that would otherwise promote attempted aggression between neighboring males. Trees, logs, and earth mounds provide shelter and structural enrichment.

Gazelles were fed *ad libitum* on dried, baled alfalfa (*Medicago sativa*) and 200–300 g Superlac concentrate per animal and day (for details see Kichenside & Lindsay, 1997). A metal shelter in each pen provided shade and protection from occasional rain. Each pen further contained a capture facility (or 'boma'), facilitating unproblematic catching of gazelles for veterinarian or management purposes. Measurements of horn length were conducted prior to our behavioral observations as part of regular veterinarian and maintenance activities; means of the measurements of both horns (left and right side) were used for the statistical analyses (see below).

Data collection

Behavioral observations at KKWRC were carried out from 11 March to 15 May 2011. We obtained data from two breeding groups of Arabian gazelles, *G. arabica* ('phenotype A' in

Wronski et al., 2010a) originating from the Arabian Peninsula (group 23: eight females, three juveniles; group 18: 11 females), two breeding groups of *G. arabica* '*farasani*', derived from animals stemming from Farasan Islands in the Red Sea (group 24: seven females and two juveniles; group 25: 10 females), two breeding groups of *G. arabica* 'phenotype B' [i.e., putative '*G. erlangeri*' (see Wronski et al., 2010a); group 29: seven females; group 1: five females and three juveniles], two breeding groups of sand gazelles, *G. marica* (group 60: nine females and one juvenile; group 65: nine females), and one group of dorcas gazelles, *G. dorcas* (five females); each breeding pen also contained one adult male.

We observed each group during eight sessions, each lasting three hours. As only one breeding group of *G. dorcas* was available, this group could be observed during 16 sessions, coming to a total observation time of 236 hours. To avoid biases caused by the circadian activity rhythm of the examined gazelles, observation sessions of each group were conducted at different times of the day (i.e., 6.00 - 9.00 a.m., 9.00 - 12.00 a.m., 12.00 a.m. - 15.00 p.m. and 15.00 - 18.00 p.m.) in random order. We observed focal groups from a vehicle, using 9 × 40 binoculars or a 25-40 × 75 spotting scope. Individuals were distinguished by individual color combinations on ear tags.

During each observation session, we used a longitudinal (all-occurrence) sampling approach (Altmann, 1974; Bateson & Martin, 1993) and recorded the following behaviors: (1) *socio-negative behaviors*: front-pressing (Walther, 1979), snout thrusting (pers. obs., this study), horn-pressing (Walther, 1979), snapping (Walther, 1964b), supplanting (Walther, 1968), body attack (Walther, 1978), chasing (Walther, 1978), low, medium, and high horn-presentation (Walther, 1968; Habibi, 1991), symbolic head- (Walther, 1979) and snout-butting (Walther, 1968); (2) *socio-positive interactions*: invitation to groom, mutual grooming, naso-nasal and naso-anal contacts (Walther, 1968).

Social network parameters and dominance indices

We constructed two social networks per sampled group using socio-positive and socio-negative interactions, separately. Thus, a total of 18 social networks was built. As our observations allowed identifying not only numbers of behaviors but also the identity of senders and receivers, the resulting networks were directed and weighted (see Whitehead, 2008). Each individual was linked to all other individuals in its social group by the observed behavioral interactions, and for each pair of individuals, the number of observed behaviors provided the weight of the link. As we observed out-going (submitted) and in-coming (received) behaviors, each individual i_i was connected to all other individuals (e.g., i_j) by two reciprocal, directed links: an out-going (from i_i to i_j) and an in-coming link (from i_j to i_i).

Following Squartini et al. (2013), one can further decompose each pair of reciprocal links into a bidirectional (fully reciprocated) interaction and a unidirectional (non-reciprocated) interaction. For example, if i_i grooms i_j 5 times, and i_j grooms i_i 3 times, the reciprocated socio-positive weight of the link is 3 while the non-reciprocated weight is 2. On the individual level, we extracted five network measures that are commonly used in studies of directed, weighted networks (see Squartini et al., 2013 for more details): (*a*) individual out-strength (sum of weights of all out-going links), which describes to what degree individuals direct socio-negative (or socio-positive) behaviors to other group members; (*b*) in-strength (sum of weights of all in-coming links), which describes to what degree individuals receive aggressive (or socio-positive) behaviors from group members; (*c*) reciprocated strength (sum of overlapping in- and out-strength), which describes the degree to which social interactions initiated by one individual will lead to a mutual response by another group member; (*d*) non-reciprocated out-strength (sum of out-strength that exceeds the reciprocated strength), which describes the degree to which initiated social interactions are not mutually responded; and (*e*) non-reciprocated in-strength (sum of in-strength that exceeds the reciprocated strength), which describes the degree to which received social interactions are not mutually responded.

On the group level, we further calculated mean network strength (mean out-strength of all individuals in a group; please note that this measure is identical to mean in-strength) as well as mean reciprocated network strength and mean non-reciprocated network strength (mean non-reciprocated out-strength, which is identical to mean non-reciprocated in-strength).

We calculated two dominance indices that can be determined for each dyad in a social network: First, we calculated the Eden (1987) index:

$DI = (W_i / T_i) / N$;

whereby N equals the total number of opponents; W_i equals the number of wins in aggressive interactions with opponent '$_i$'; and T_i equals the total number of aggressive interactions with opponent 'i'.

Secondly, we calculated the Clutton-Brock et al. (1979) index of fighting success as:

$IFS = B + \Sigma b + 1/L + \Sigma l + 1$;

where B is the number of females in a group that are dominated by the focal animal, Σb is the total number of females dominated by them excluding the focal female, L is the number of females who dominated the focal female, and Σl is the total number of females which dominated them excluding the focal female.

We also tested for linearity in the dominance hierarchy of our study animals. Landau's index of linearity (Landau, 1951) was calculated as follows:

$h = (12/n^3 - n)\ \Sigma\ [v_a - (n - 1) / 2]^2$;

whereby n equals the number of animals in the group; v_a equals the number of animals that an individual dominated (v_a was derived from the network of dominance indices (Eden index). According to Bekoff (1977) and Chase (1974), a linearity index of $h \geq 0.9$ is a reasonable cut-off criterion for a strong, nearly linear hierarchy.

Statistical analysis

Data sets of all network parameters violated the assumptions of normal distribution and homoscedasticity, and no transformation could improve their distribution. We, therefore, decided to use non-parametric statistics throughout. First, we tested for an effect of inter-individual variation in horn length on social network parameters (i.e., in-strength, out-strength, reciprocated strength, non-reciprocated out-strength and non-reciprocated in-strength) within groups using Spearman rank correlations.

Second, we tested for differences in average horn length and group averages of network metrics. A Kruskal-Wallis ANOVA was employed to test for differences among groups in median horn length, and to test for differences in median values of social network parameters. We employed all-pairwise Dunn's *post-hoc* tests to identify the source of variation in case of significant results.

Third, we used group means of horn length and mean network strength, mean reciprocated network strength, and mean non-reciprocated network strength for additional correlation analyses. Group means of those variables were correlated with mean horn lengths of the different groups using Spearman rank correlations. We corrected for inflation of type I errors due to multiple comparisons (i.e., several correlation analyses within the same group) by adjusting significance levels as $\alpha' = \alpha$ / number of multiple comparisons (Bonferroni-correction).

Finally, we applied non-parametric Spearman rank correlations between mean group horn length and group dominance indices (see above) for all female breeding groups included in our study. Significance levels were corrected for multiple testing of the same group as $\alpha' = 0.05 / 2 = 0.025$.

RESULTS

Numbers of aggressive behaviors per hour observation ranged from 0.6 (group 29) to 3.1 (group 23) in the different groups of gazelles studied here, and numbers of socio-positive behaviors ranged from 6.1 (group 60) to 0.5 (group 25). We used those behaviors to calculate various indices characterizing dominance hierarchies. Spearman rank correlations of network parameters and inter-individual variation in horn length within groups detected no significant effects of horn length on network parameters calculated from socio-positive behaviors (Table 1; Figure 2.). In the case of aggressive behaviors, few cases (four out of 45 correlations) were found in which inter-individual variation in horn length tended to affect network parameters (i.e., $0.01 < p < 0.05$), but none of those effects were significant after Bonferroni-correction for multiple testing of the five network parameters in each group (Table 1). A similar pattern was apparent when considering dominance indices [Eden's (1987) index, Clutton-Brock's (1979) index; Table 2]. Hence, we found no evidence for a consistent effect of inter-individual variation in horn length within groups on any of the five network parameters or dominance indices considered in this study, suggesting that differences among female group members in horn length did not affect their social network position and dominance stratification.

FIGURE 2, TABLE 1 , 2

When comparing individual attributes of horn length and network parameters between groups, a Kruskal-Wallis ANOVA detected pronounced variation in median horn length, ranging from 3.3 cm (interquartile range, IQR = 0.0 to 7.1 cm) in *G. arabica farasani* (group 24) to 21.0 cm (IQR = 18.8 to 22.9 cm) in *G. marica* (group 65; Figure 3). At the same time, network parameters showed significant variation among groups, the only exceptions being non-reciprocated in- and out-strength calculated from socio-negative behaviors (Table 3). When we tested for correlations between group means of network parameters, none of the network parameters calculated from socio-negative behaviors showed any significant effect (Table 4). The same was true for Landau's (1951) index of linearity (Spearman rank correlation: $r = 0.033$, $p = 0.91$, $N = 9$). These results suggest that—even though major differences in most network parameters were apparent—average horn length of a group did not predict the nature of dominance hierarchy stratifications and overall aggression.

FIGURE 3, TABLE 3

When considering network parameters derived from socio-positive behaviors, however, a significant effect of horn length was found in the case of reciprocated network strength, which decreased with increasing horn length ($r = -0.74$, $p = 0.016$; Figure 4), and this effect remained statistically significant after Bonforroni-correction (Table 4). Hence, in groups with longer horns, individuals had fewer reciprocated socio-positive interactions. A non-significant tendency was detected for mean network strength to decrease with increasing horn length ($r = -0.63$, $p = 0.058$; Table 4; Figure 4). Taken together, greater average horn length in female groups appears to be coupled with fewer socio-positive interactions—which translates into fewer reciprocated interactions—among group members.

FIGUE 4 , TABLE 4

CONCLUSION

Function of female horns in gazelles

We formulated a set of predictions derived from two hypotheses seeking to explain the evolution of female horns in bovids: predictions (*a*)–(*e*) tested the 'female competition hypothesis' (Roberts, 1996) and assumed network parameters and dominance indices calculated from socio-negative behaviors to correlate with inter-individual variation in horn length within, or variation in mean horn length between groups. We found no support for either of those predictions, and so our results suggest that female horns are not primarily used in aggressive interactions between females, i.e., in the formation of dominance relationships. Alternative predictions were derived from the 'andromimicry hypothesis' (Estes, 1991, 2000, 2011): while prediction (*f*) also assumed elevated levels of aggression to occur in groups with longer horns (for which no support was found), prediction (*g*) was confirmed in that network parameters derived from socio-positive behaviors (network strength and reciprocated network strength) decreased with increasing (group-level) horn length.

Our interpretation rests upon the assumption that additional hypotheses for the evolution of female horns (the 'predator defense hypothesis': Darling, 1937; Packer, 1983; Stankowich & Caro, 2009 and the 'intra-specific competition hypothesis': Geist, 1974a, b, 1977; Janis, 1982) are not necessarily mutually exclusive. In other words, besides the potential benefits of developing male-like female weaponry that we will outline below (when discussing how our data support the 'andromimicry hypothesis'), additional benefits of well-developed female weaponry may arise, e.g., from the ability to better fend off sexually harassing males. Male sexual harassment of females has been described from a number of bovids (Reduncini: Estes 1991; Tragelaphini: Walther, 1964a; Apio et al., 2007), including the Antilopini tribe (e.g., Thomson's gazelle, *Eudorcas thomsoni*: Walther, 1964b; Grant's gazelle, *Nanger granti*: Walther, 1965). Tests of those potential additional functions of female horns in the species of true gazelles studied here will be reserved for future studies. Moreover, we discuss the results from our present study with caution as our study suffers from a potential short-coming in that we did not compare independently evolving phylogenetic lineages (i.e. species). Instead, our statistical analyses had to rely on a comparison of different breeding groups belonging to three *Gazella* species, one of which (*G. arabica*) comprised phenotypic variation at the population/subspecies level. Our study was restricted by the availability of different gazelle taxa available at KKWRC, and we refrained from including additional *Gazella* groups held under dissimilar climatic and general maintenance conditions at other breeding centers, as including data from such groups would have introduced a substantial source of variation to the data.

Following the classical literature on fighting behavior (e.g., Lorenz, 1963) one would expect that taxa with more-developed weaponry (large antlers and horns, etc.)—which are more likely to cause severe injuries—should show less overt aggression, and fighting should be ritualized. In a logic extension of this argument, we would have expected socio-positive behaviors to increase in long-horned groups, but the opposite effect was observed. However, our findings are in good agreement with our prediction (*g*) that was derived from the 'andromimicry hypothesis' (Estes, 1991, 2000, 2011). The latter hypothesis was formulated based on the following observations: In ungulate species in which horns emerge within the first few months of age (like eland, *Tragelaphus oryx*), both sexes are horned, but in species in which horns emerge much later, only males have horns (greater kudu, *T. strepsiceros*: Darwin, 1874). Moreover, in species with hornless females, breeding males consider young males as potential rivals once their horns emerge and drive them away from female herds or territories. This, in turn, will lead to a higher juvenile mortality, as young males no longer receive protection from their mother or other members of their natal herd. By contrast, when young bear similar horns in both sexes, horns are no longer indicative of offspring sex. Selection acting on females to keep their sons inside their natal herds until they have grown to the stage where they benefit more from joining bachelor herds can thus promote mimicry of male horns and other male secondary sexual characters, such as male color patterns (Estes, 2000). Based on our present study, we tentatively argue that female true gazelles may not only evolve morphological traits resembling the male sex (i.e., horns) but also adopt male-like behavior, i.e., both character suites coevolve. While such a scenario seems plausible to explain decreasing socio-positive behavior with increasing degree of female horn-development [prediction (*g*)], it remains elusive why aggressive behavior was not increased [prediction (*f*)]. Revisiting our previous assertion that stronger weaponry is associated with a higher likelihood of incurring injuries, which should select for reduced overt aggressive behavior (especially non-ritualized fighting behavior; e.g., Lorenz, 1963) we tentatively argue that this explains best why gazelle females in long-horned clades mimic males only by reducing socio-positive behavior, but not by increasing socio-negative behavior.

If we accept this line of argumentation, another, more general question emerges: how can we explain why females mimic males in morphology and behavior and some, but not all clades of true gazelles? We follow Estes' (2000) line of argumentation, which was formulated, for instance, to explain the evolution of male-like characters (like darkened fur coloration) in female sable antelope (*Hippotragus niger*). We argue that species with long female horns, such as *Gazella marica* (included in this study) and *G. leptoceros* (not included here), inhabit open habitat types with the least precipitation amongst the true gazelles. Those species tend to form larger herds, partly because resources are unevenly distributed and groups migrate in search of new pasture, while other species of true gazelles inhabit mountainous habitats with woody vegetation and more continuous resource availability (*G. gazella*, *G. arabica*, *G. cuvieri*; Lerp et al., 2016). Higher costs of living outside the herd in open-land dwellers increase the benefits arising from the prolonged presence of male offspring in their natal herds, giving rise to the emergence of male-like traits in females. However, the degree of andromimicry in open-land dwelling true gazelles is sometimes even opposite to this pattern, as female goitred gazelles (*G. subgutturosa*) have no horns at all (Kingswood & Blank, 1996). Possibly, selection favoring andromimicry was temporarily interrupted or weakened by succeeding interglacial periods, which brought about periods of warmer and moister climate in today's Central Asian steppes (Fowell et al., 2003; Zhaoa et al., 2009).

Female aggressiveness in captive breeding groups of true gazelles

The breeding stock of gazelles at King Khalid Wildlife Research Centre serves as a genetic reservoir for three highly threatened species (*G. marica*, *G. dorcas* and three phenotypically distinct forms of *G. arabica*) and as a source to supplement wild populations. Breeding groups are composed of one adult male and a number of females to ensure maximum reproduction and an adequate stock of animals to be released into the wild at any time. To ensure optimal breeding conditions, animal welfare, and health, group compositions and group sizes of gazelles held at KKWRC are close to what is reported from the wild (Kingswood & Blank, 1996; Yom-Tov et al., 1995; Cunningham & Wronski, 2011b). Captive-raised animals may be less able to survive and reproduce after release than wild-born, translocated, conspecifics. Indeed, reintroductions using wild populations as the source are approximately twice as successful as those using captive-born animals (Griffiths et al., 1989; Fischer & Lindenmayer, 2000). If captive individuals lack behavioral competencies, aberrant behavior may prevail and can hamper the reintroduction success (Beck et al. 1994; Beck, 1995). Stoinski and Beck (2004) reported on a failed reintroduction attempt due to changes in the locomotor and foraging skills of captive-born golden lion tamarins (*Leontopithecus rosalia*) reintroduced into Brazilian Atlantic forest. Beck (1995) suggested that captive breeding facilities (such as KKWRC) should prepare animals to cope with the challenges they will face in the wild by exposing them to various opportunities and impediments prior to the release.

In captive-bred ungulates, one of the major behavioral competencies to adopt is the ability to form a natural social organization, including the ability to form a dominance hierarchy within the herd. In their natural habitats, members of a herd can either disperse or challenge the dominant individual, but are always able to avoid aggression and combat. In our study we raised the questions: are female gazelles more aggressive in captive groups? Is there any unusual structure in their social network organization (e.g., do few animals receive all socio-negative attention)? Suboptimal rearing conditions and artificial group structures can lead to increased levels of aggressive behaviors amongst the members of captive breeding groups (Calhoun, 1962; Christian, 1963; Morgan & Tromborg, 2007) and may thus impede the success of a reintroduction attempt (which in itself is also stressful). Matthews et al. (2005) suggested pre-release screening protocols in which behaviors of wild conspecifics provide the baseline.

Controlled behavioral experiments should be used to assess the suitability for release of specific captive-bred individuals, and animals that show aberrant behavior should not be released.

Female Antilopini (whether short-horned or long-horned, whether migratory and aggregative or rather solitary) typically form dominance hierarchies, which is also reflected by individuals maintaining distances of 1-3 m while foraging or during filing and resting bouts (Walther et al., 1983). Also female *G. dorcas*, *G. arabica* and *G. marica* establish dominance hierarchies in wild populations using a number of aggressive behaviors, such as horn-threats, rush-charges, horn-clashing, butting and chasing (Kingswood and Blank, 1996; this study). Still, while male Antilopini show pronounced aggressiveness and territorial behavior (Walther, 1978, 1979; Walther et al., 1983), aggressive behaviors are rare among females (Walther 1972). Although behavioral studies on female gazelles in the wild are scarce, moderate levels of aggressiveness, as seen in our present study, do not appear to be higher than what can be found in the wild. Hence, there are no obvious signs of adverse effects arising from the captive breeding scheme at KKWRC on the behavioral competency of gazelles. Similar observations were reported from multi-species breeding groups in Al Wabra Wildlife Preservation (AWWP) in Qatar. A study reporting mortality patterns and husbandry management of female breeding groups of various gazelles held at AWWP found trauma, which is indicative of severe aggressive interactions, to make up only 16-20% of the causes of death at the breeding center (Dünner et al., 2010a).

The results from our social network analyses suggest that there was pronounced variation in dominance stratifications amongst groups, pointing towards flexibility in network structures, but there was no indication for obviously aberrant social network structures. The same is true when comparing dominance indices between breeding groups and species. Altogether then, it appears that the breeding stock kept at KKWRC is well suited for reintroductions from a behavioral perspective. Breeding conditions at KKWRC seem to support the wellbeing of gazelles, which includes a sufficient size of the breeding pens, their structural enrichment and the remoteness of the center, leading to very little human disturbance and, therefore, low stress levels. Moreover, husbandry management and physical constraint for veterinary care are limited to a minimum at KKWRC (Kichenside & Lindsay, 1997; Mohammed et al., 2010). Reports from other breeding centers on the Arabian Peninsula indicate that group structure and composition also have a pronounced effect on the wellbeing of gazelles. In AWWP all available females were used for breeding until 2003 and kept in breeding groups just like those established at KKWRC. To reduce breeding, single-sex groups were established in 2004. It became evident that in 2004 the number of animals which died due to a trauma was noticeable higher in males, while the new maintenance conditions left the rates of trauma in female groups unchanged or even reduced female mortality rates (Dünner et al., 2010b).

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TABLES

Table 1

Non-parametric Spearman rank correlations between individual network metrics calculated from (*a*) socio-negative and (*b*) socio-positive behaviors for all dyadic interactions among females in breeding groups held at King Khalid Wildlife Research Center. Significance levels were corrected for multiple testing of the same group as α' = 0.05 / 5 = 0.01; results with $p < 0.05$ (not significant after Bonferroni-correction) are marked in boldface.

	***farsani*24**		***farasani*25**		***erlangeri*29**		***erlangeri*1**		***arabica*23**		***arabica*18**		***dorcas***		***marica*60**		***marica*65**	
	N = 7		*N* = 10		*N* = 7		*N* = 5		*N* = 8		*N* = 11		*N* = 4		*N* = 9		*N* = 9	
SOCIO-NEGATIVE	*r*	*p*	*r*	*p*	*r*	*p*	*r*	*p*	*r*	*p*	*r*	*p*	*r*	*p*	*r*	*p*	*r*	*p*
Out-strength	0.36	0.39	0.21	0.54	-0.36	0.39	-0.60	0.35	0.57	0.12	**0.59**	**0.05**	-0.40	0.75	-0.28	0.43	-0.55	0.11
In-strength	0.69	0.08	-0.32	0.35	0.14	0.72	0.30	0.68	**-0.73**	**0.03**	-0.15	0.65	0.40	0.75	-0.10	0.76	0.28	0.43
Reciprocated strength	0.22	0.61	0.37	0.28	-0.49	0.22	-0.32	0.52	0.49	0.21	0.21	0.52	0.40	0.75	-0.38	0.29	**-0.72**	**0.03**
Non-reciprocated out-strength	0.36	0.39	0.18	0.61	-0.38	0.39	-0.60	0.35	0.55	0.14	0.52	0.10	-0.40	0.75	-0.30	0.41	-0.46	0.19
Non-reciprocated in-strength	**0.74**	**0.04**	-0.35	0.31	0.21	0.60	0.30	0.68	**-0.74**	**0.03**	-0.26	0.42	0.40	0.75	-0.07	0.84	0.32	0.38
SOCIO-POSITIVE																		
Out-strength	-0.43	0.30	-0.29	0.38	0.11	0.78	0.29	0.68	0.38	0.32	0.23	0.48	-0.74	0.33	< 0.01	1.00	-0.55	0.11
In-strength	-0.05	0.91	0.10	0.76	-0.04	0.91	0.29	0.68	-0.25	0.50	-0.35	0.28	0.32	0.75	< 0.01	1.00	0.41	0.24
Reciprocated strength	-0.56	0.15	< 0.01	1.00	-0.32	0.44	0.29	0.68	< 0.01	1.00	0.12	0.71	< 0.01	1.00	< 0.01	1.00	< 0.01	1.00
Non-reciprocated out-strength	-0.43	0.30	-0.29	0.38	0.19	0.67	< 0.01	1.00	0.38	0.32	0.11	0.73	-0.74	0.33	< 0.01	1.00	-0.55	0.11
Non-reciprocated in-strength	0.29	0.49	0.10	0.76	0.02	0.91	< 0.01	1.00	-0.25	0.50	-0.54	0.08	0.32	0.75	< 0.01	1.00	0.41	0.24

Table 2

Non-parametric Spearman rank correlations between group means of horn length and dominance indices (see above) for all female breeding groups included in our study. Significance levels were corrected for multiple testing of the same group as α’ = 0.05 / 2 = 0.025; results with $p < 0.05$ (not significant after Bonferroni-correction) are marked in boldface.

	***farsani*24** *N* = 7		***farasani*25** *N* = 10		***erlangeri*29** *N* = 7		***erlangeri*1** *N* = 5		***arabica*23** *N* = 8		***arabica*18** *N* = 11		***dorcas*** *N = 4*		***marica*60** *N* = 9		***marica*65** *N* = 9	
	r	*p*	*r*	*p*	*r*	*p*	*r*	*p*	*r*	*p*	*r*	*p*	*r*	*p*	*r*	*p*	*r*	*p*
Eden index	-0.40	0.34	0.25	0.47	-0.36	0.39	-0.80	0.13	**0.74**	**0.03**	0.29	0.38	0.10	0.95	0.12	0.74	-0.18	0.61
Clutton-Brock index	-0.52	0.18	0.22	0.51	-0.25	0.55	-0.70	0.23	0.64	0.07	0.58	0.06	0.15	0.78	0.15	0.68	-0.05	0.88

Table 3

Results from non-parametric Kruskal Wallis *H*-tests (followed by *post hoc* all-pairwise Dunn's tests, shown are significant differences with $p < 0.05$) demonstrating significant variation among the investigated groups of gazelle females in median horn length and group-level network metrics calculated from socio-negative and socio-positive behaviors (see main text for details). $df = 8$ in all cases. Significant effects are marked in boldface [(*) $0.05 < p < 0.1$; * $p < 0.05$; ** $p < 0.01$; *** $p < 0.001$].

	H	***p***	**Dunn's test**
HORN LENGTH	**52.88**	**< 0.001*****	m60 > f24, e29, e1, a18, m65 > f24, e29, e1, a18, d > f24, e29
SOCIO-NEGATIVE			
Out-strength	**21.17**	**0.007****	a18 > e29
In-strength	**17.46**	**0.026***	a18 > e29
Reciprocated strength	**38.84**	**< 0.001*****	a18 > e29, e1, a23, m60, m65
Non-reciprocated out-strength	**15.05**	**0.058(*)**	
Non-reciprocated in-strength	12.72	0.122	
SOCIO-POSITIVE			
Out-strength	**20.90**	**0.007****	
In-strength	**25.97**	**0.001****	e29 > m60
Reciprocated strength	**16.11**	**0.041***	
Non-reciprocated out-strength	**21.28**	**0.006****	
Non-reciprocated in-strength	**22.36**	**0.004****	

Table 4

Spearman rank correlations between mean (group-level; $N = 9$) horn length and mean values of different network metrics calculated from socio-negative and socio-positive behavioral interactions. α-levels were corrected as $\alpha' = 0.05/3 = 0.017$; significant effects are marked in boldface [(*) $0.05 < p < 0.1$; * $p < 0.05$].

	Network strength		**Reciprocated strength**		**Non-reciprocated strength**	
	r	*p*	*r*	*p*	*r*	*p*
SOCIO-NEGATIVE	0.10	0.78	0.001	0.78	0.13	0.71
SOCIO-POSITIVE	**-0.63**	**0.058(*)**	**-0.74**	**0.016***	-0.39	0.29

FIGURES

Figure 1

Variation in female horn-length within and among groups of true gazelles (*Gazella* spp.) held at King Khalid Wildlife Research Center in Saudi Arabia. Shown are exemplary breeding groups of (*a*) *G. arabica farasani* (photographed in their natural habitat), (*b*) *G. arabica*, (*c*) *G. dorcas*, (*d*) putative *G. erlangeri*, and (*e*) *G. marica*.

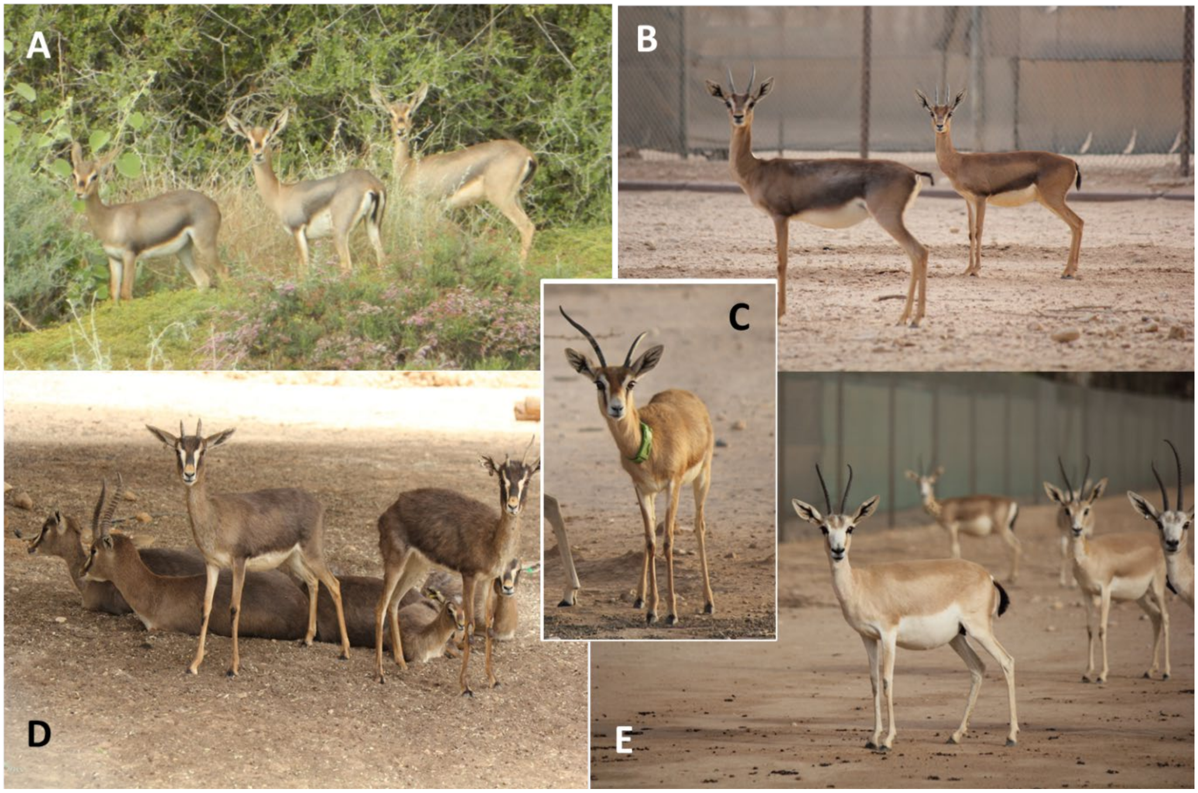
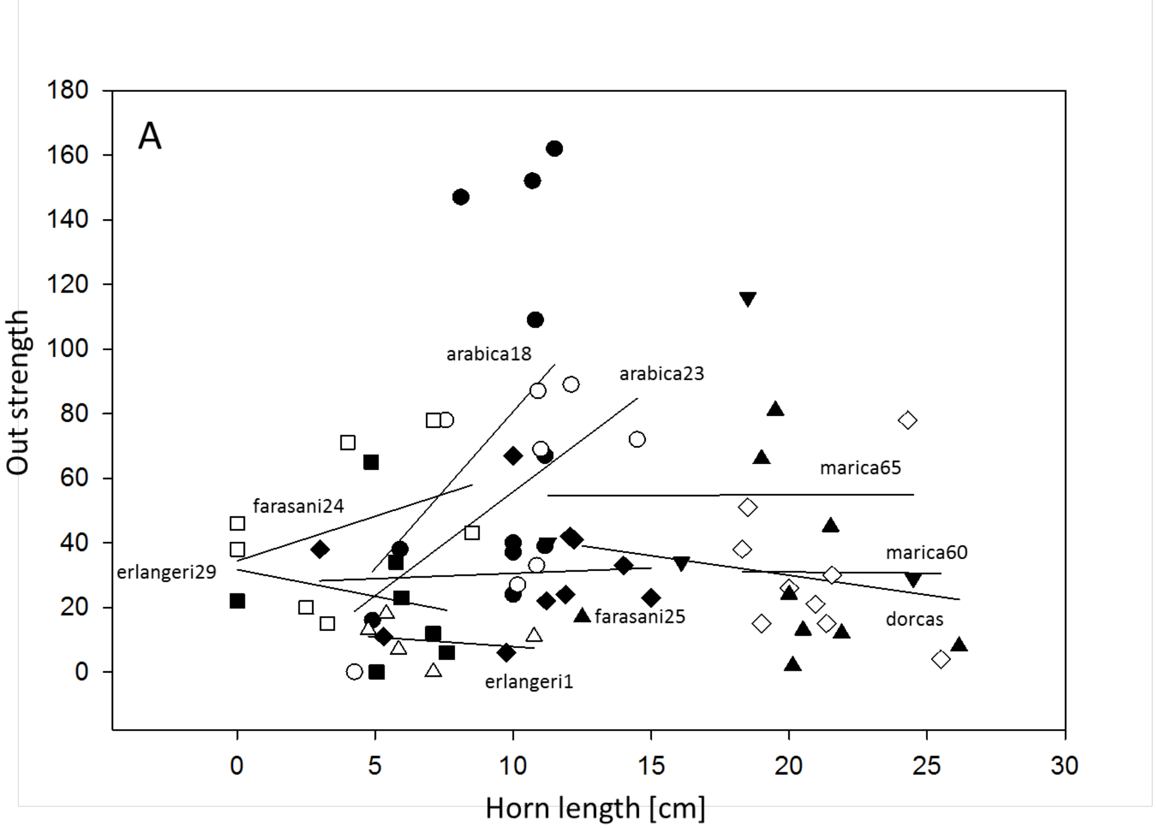
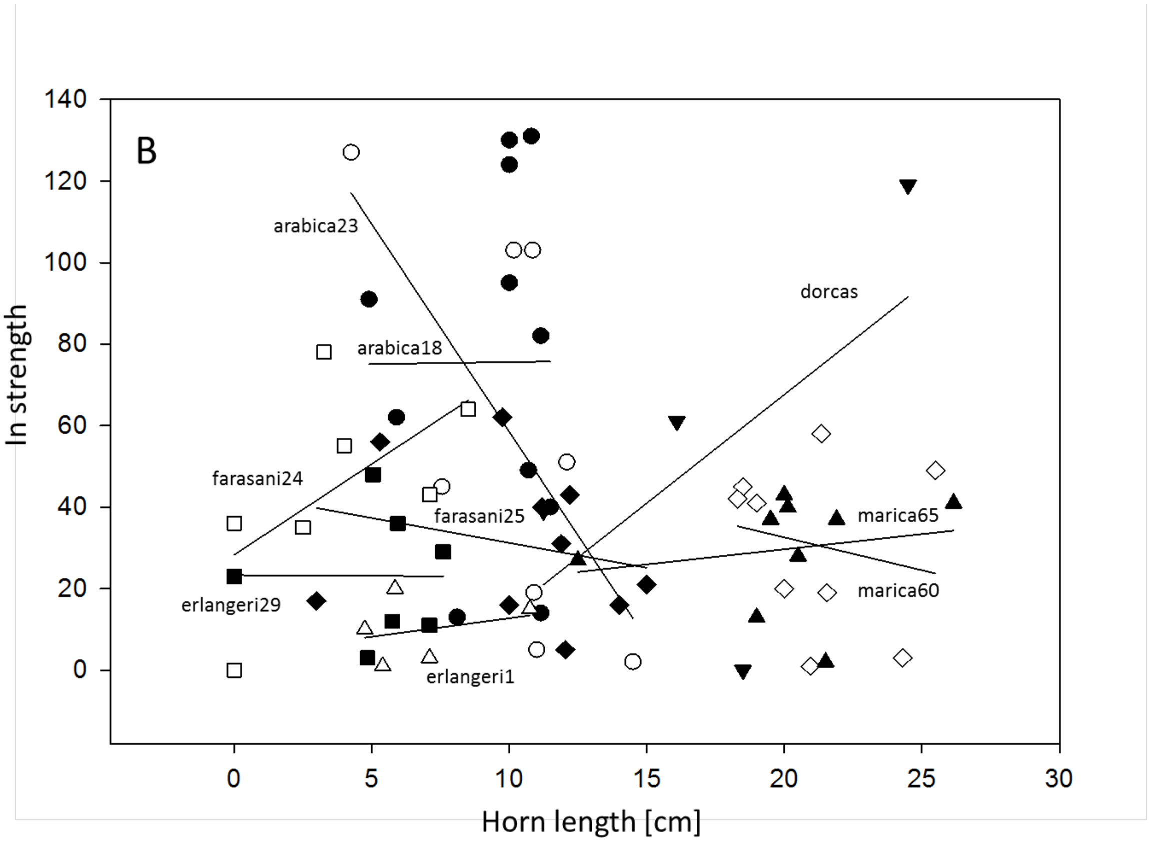
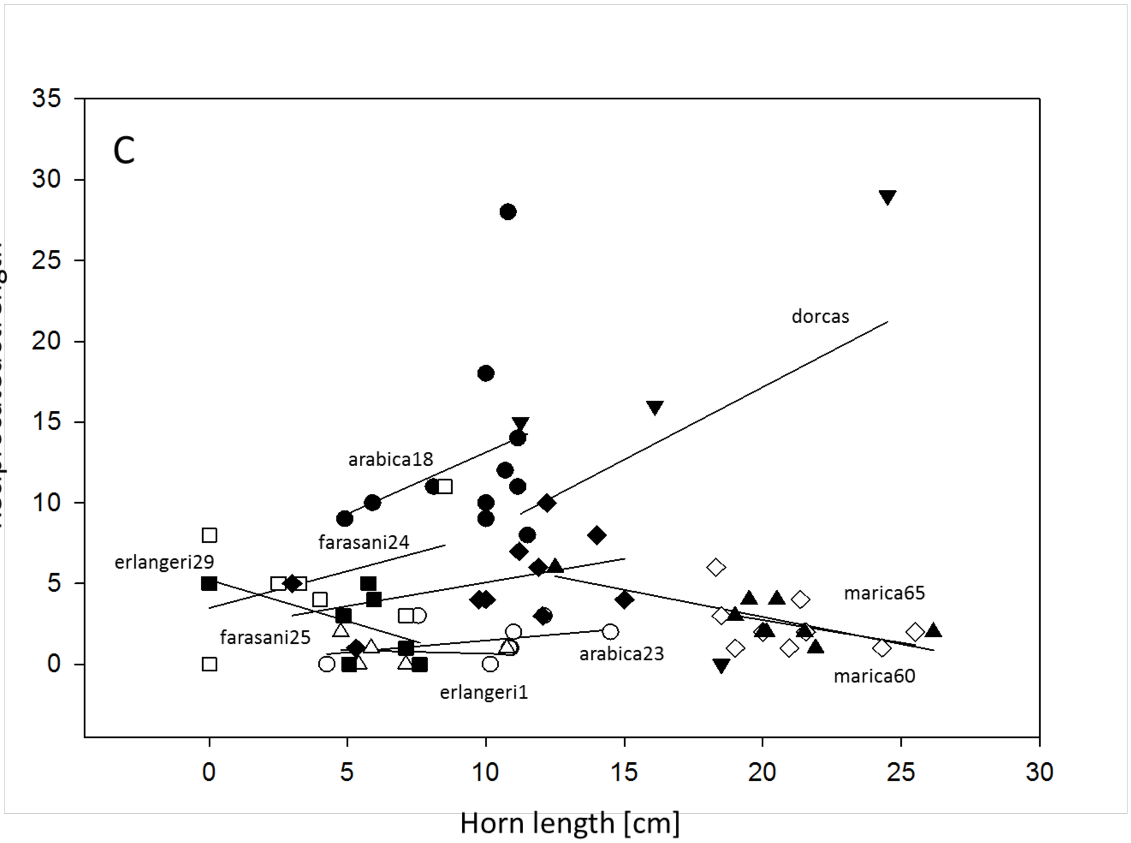


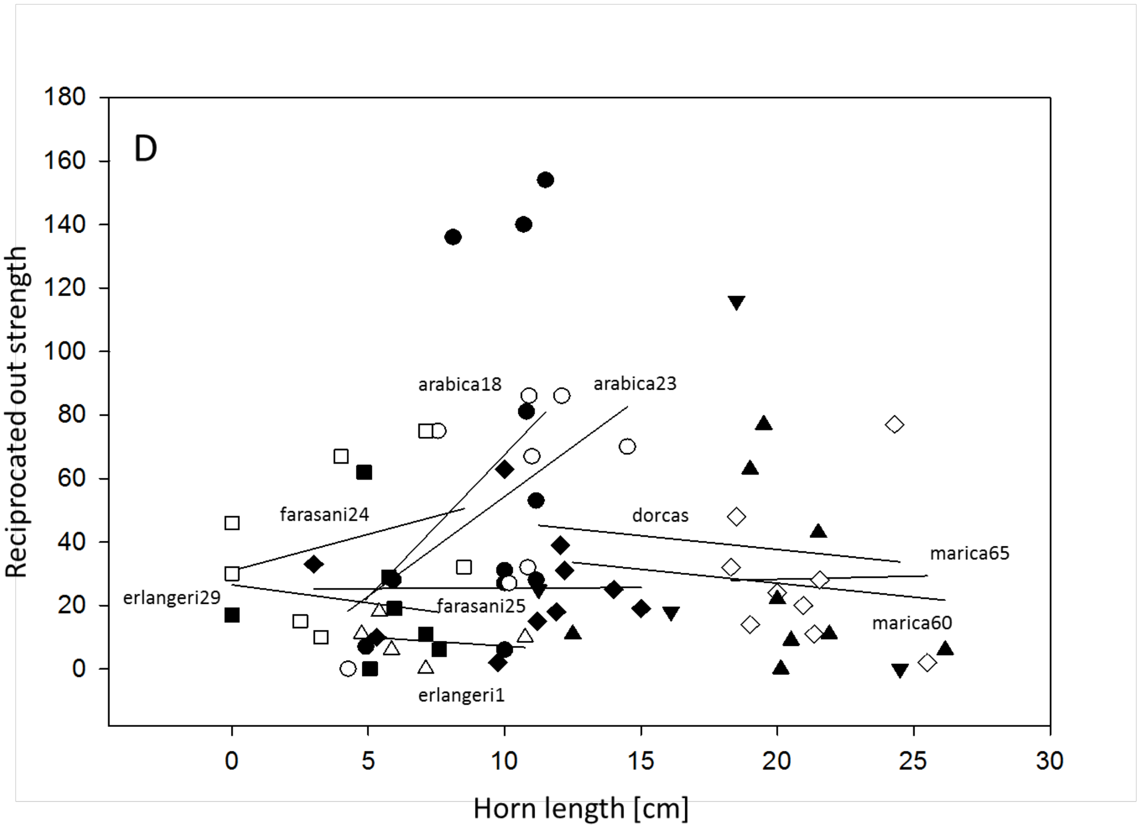
Figure 2

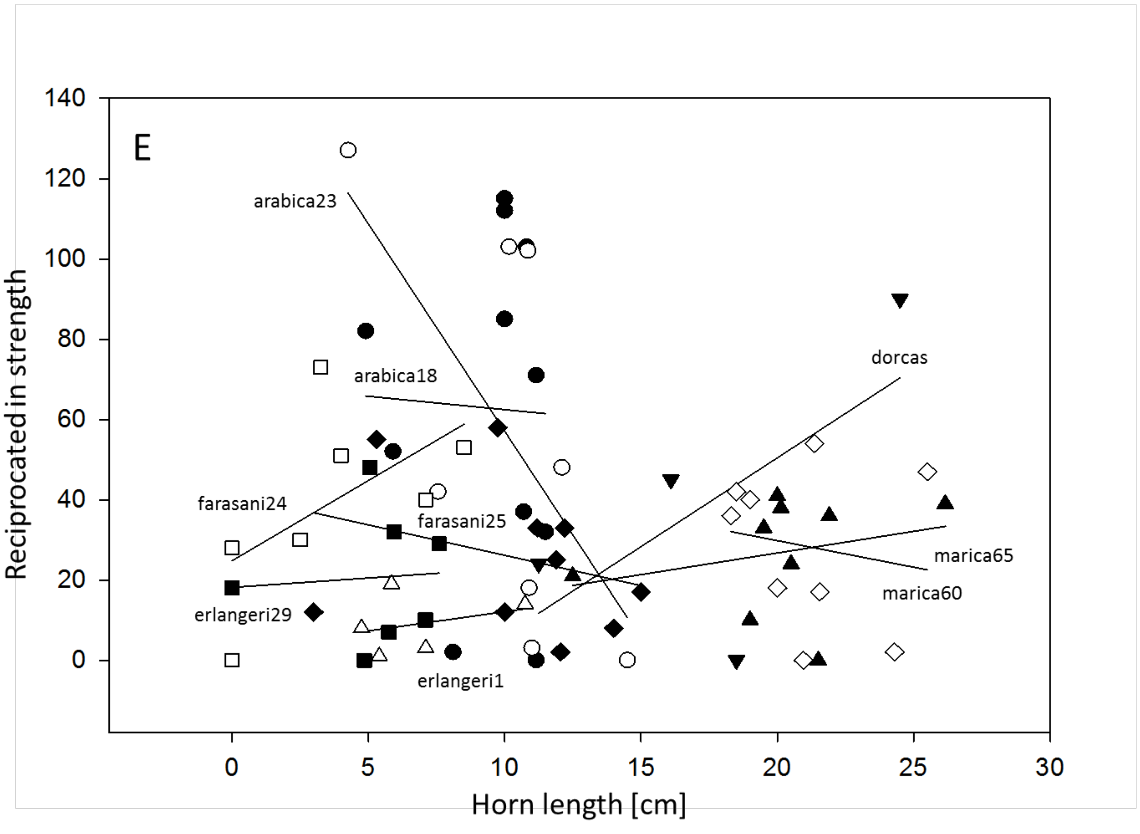
Relationship between horn length and five network parameters [individual out-strength (sum of weights of all out-going links), in-strength (sum of weights of all in-coming links), reciprocated-strength (sum of overlapping in- and out-strength), non-reciprocated out-strength (sum of out-strength that exceeds the reciprocated-strength), and non-reciprocated in-strength (sum of in-strength that exceeds the reciprocated-strength]. Shown are network metrics calculated from socio-negative interactions (*a–e*), and socio-positive interactions (*f–j*) for nine groups of captive gazelles kept at KKWRC: *G. arabica farasani* (group 24; □), *G. arabica farasani* (group 25; ♦), putative *G. erlangeri* (group 29; ■), putative *G. erlangeri* (group 1; Δ), *G. arabica* (group 23; ○), *G. arabica* (group 18; ●), *G. dorcas* (▼), *G. marica* (group 65; ▲), *G. marica* (group 60; ◊).

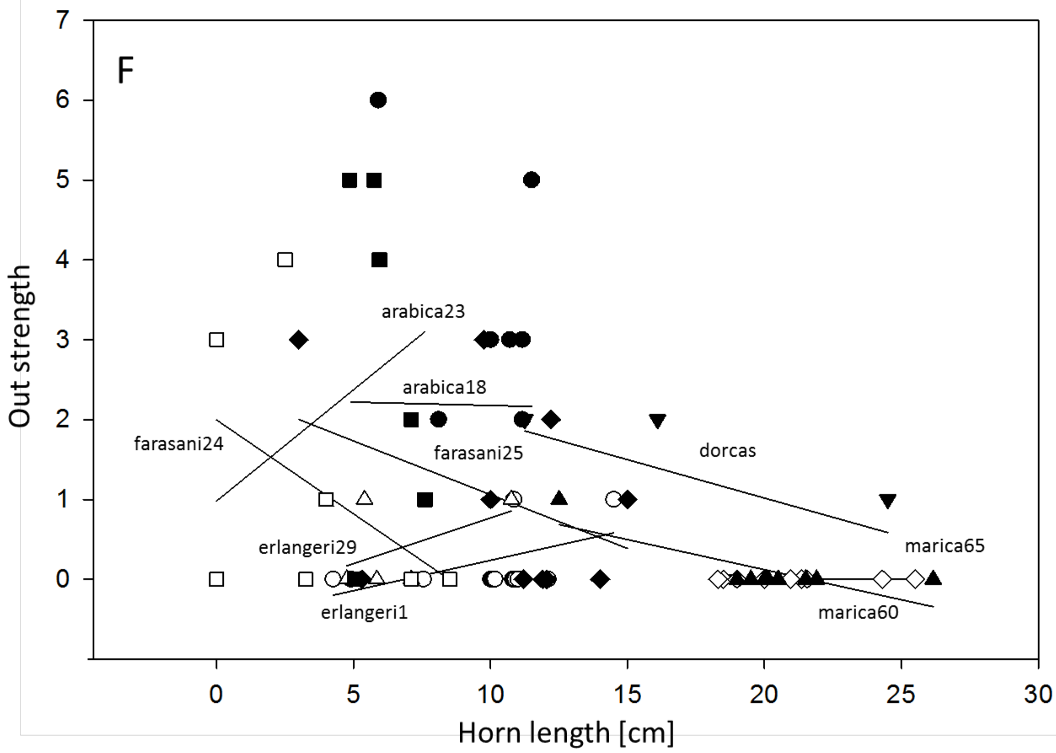


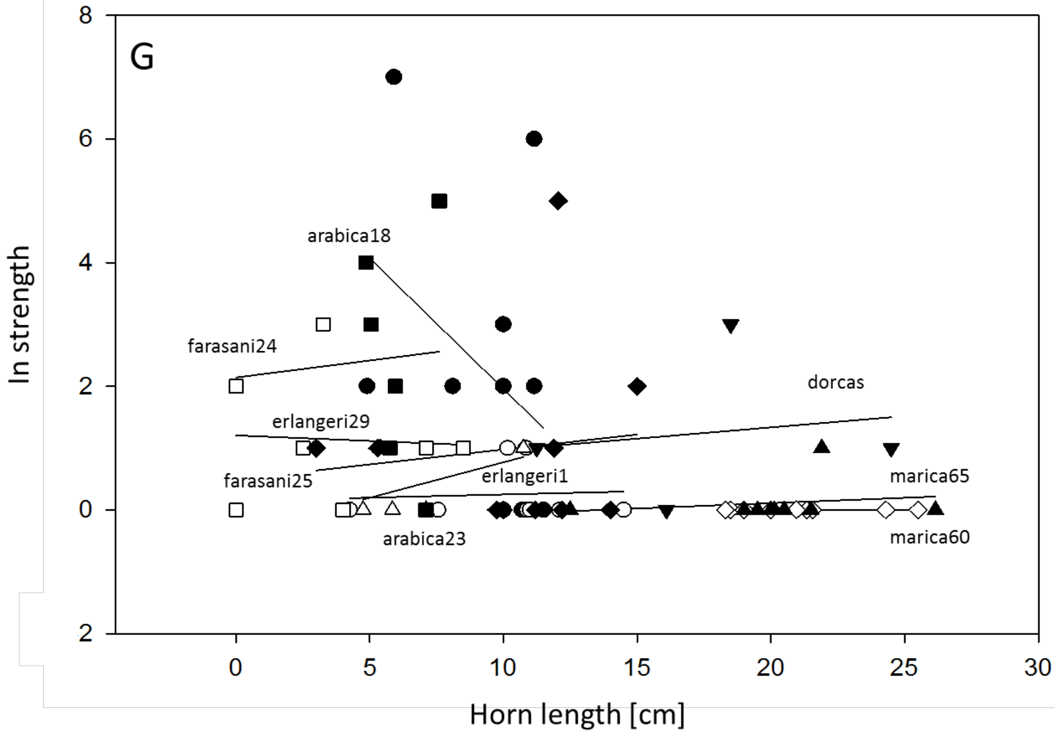

B
In strength
140
120
100
80
60
40
20
0
Horn length [cm]
0
5
10
15
20
25
30
arabica23
arabica18
dorcas
farasani24
farasani25
marica65
erlangeri29
marica60
erlangeri1

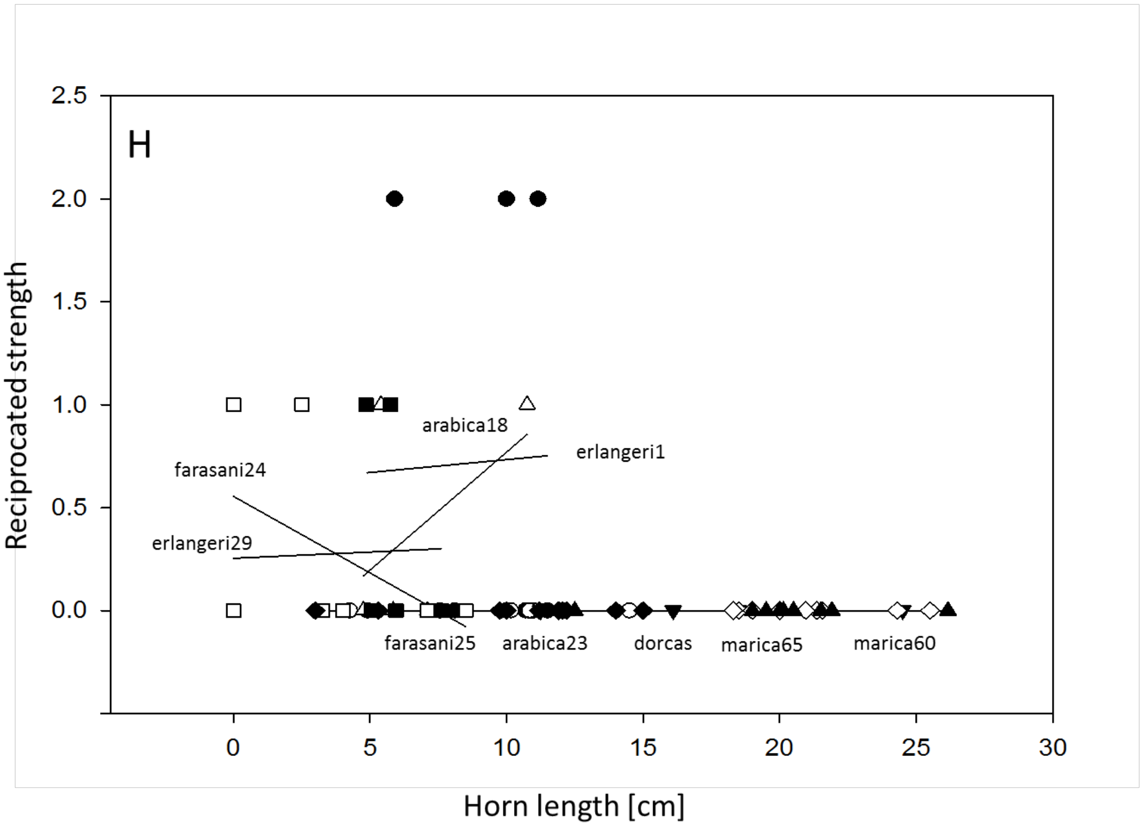

C
Reciprocated strength
35
30
25
20
15
10
5
0
Horn length [cm]
0
5
10
15
20
25
30
dorcas
arabica18
farasani24
erlangeri29
marica65
farasani25
arabica23
marica60
erlangeri1

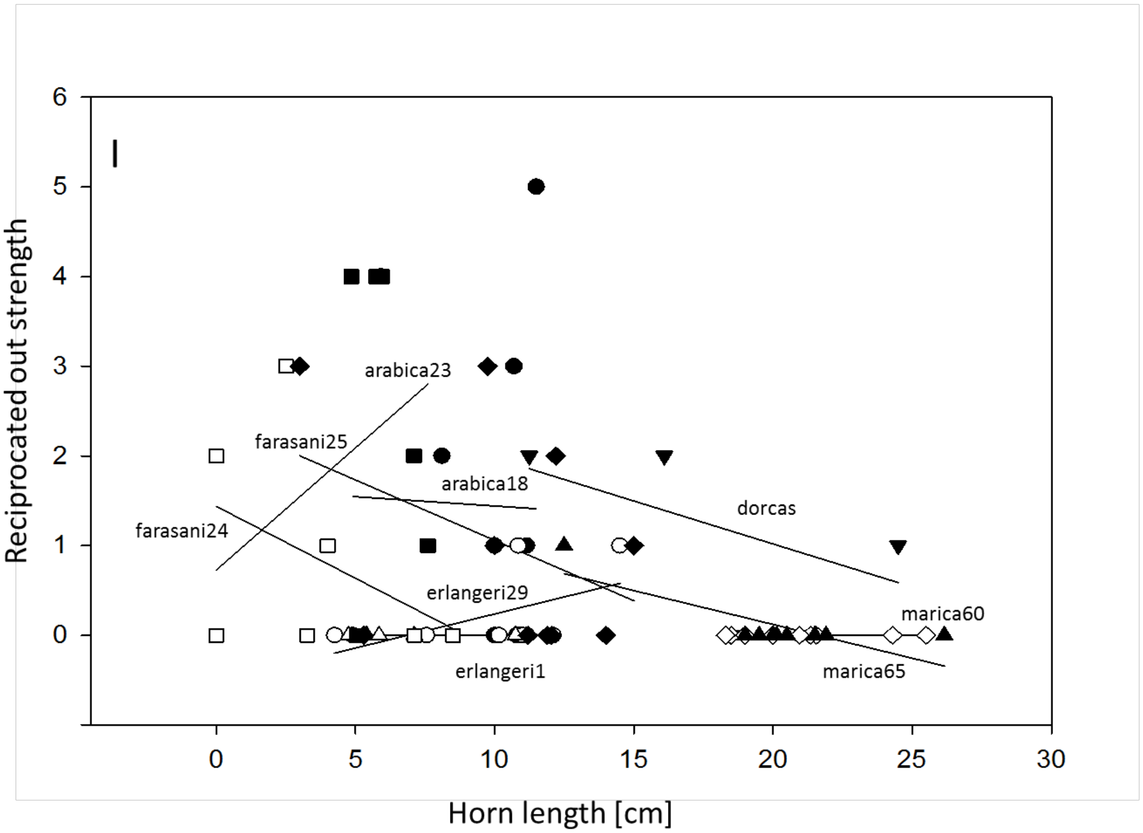

D
Reciprocated out strength
Horn length [cm]
180
160
140
120
100
80
60
40
20
0
0
5
10
15
20
25
30
arabica18
arabica23
farasani24
dorcas
marica65
erlangeri29
farasani25
marica60
erlangeri1


E
Reciprocated in strength
Horn length [cm]
140
120
100
80
60
40
20
0
0
5
10
15
20
25
30
arabica23
arabica18
dorcas
farasani24
farasani25
marica65
marica60
erlangeri29
erlangeri1


F
Out strength
7
6
5
4
3
2
1
0
0
5
10
15
20
25
30
Horn length [cm]
arabica23
arabica18
farasani24
farasani25
dorcas
erlangeri29
marica65
erlangeri1
marica60


G
In strength
8
6
4
2
0
2
0
5
10
15
20
25
30
Horn length [cm]
arabica18
farasani24
dorcas
erlangeri29
farasani25
erlangeri1
marica65
arabica23
marica60


H
Reciprocated strength
2.5
2.0
1.5
1.0
0.5
0.0
arabica18
erlangeri1
farasani24
erlangeri29
farasani25
arabica23
dorcas
marica65
marica60
0
5
10
15
20
25
30
Horn length [cm]


I
Reciprocated out strength
6
5
4
3
2
1
0
arabica23
farasani25
arabica18
dorcas
farasani24
erlangeri29
marica60
erlangeri1
marica65
0
5
10
15
20
25
30
Horn length [cm]

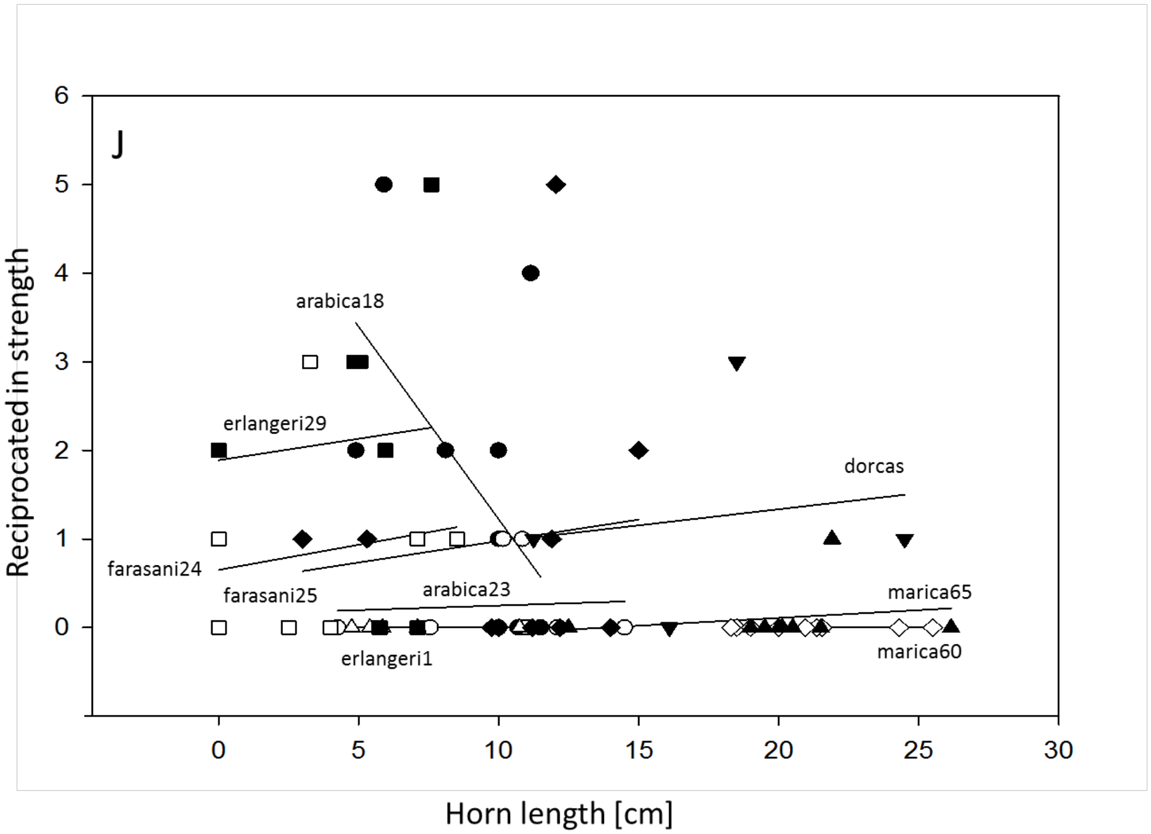

J
Reciprocated in strength
Horn length [cm]
0
1
2
3
4
5
6
0
5
10
15
20
25
30
arabica18
erlangeri29
dorcas
farasani24
farasani25
arabica23
marica65
erlangeri1
marica60

Figure 3
Variation in median horn length between *G. arabica farasani* (groups 24, 25), putative *G. erlangeri* (groups 1, 29), *G. arabica* (groups 18, 23), *G. marica* (groups 60, 65) and *G. dorcas*.

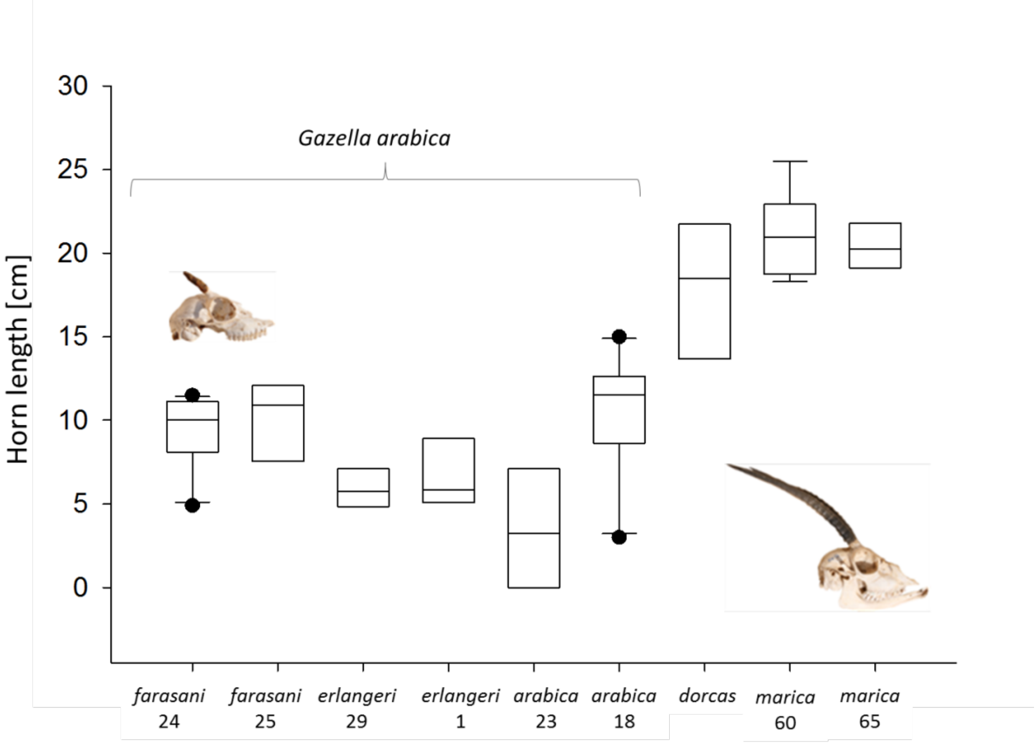


Figure 4
Scatter plots illustrating the relationship between mean horn-length (group means) and mean values of network parameters (a, network strength; b, reciprocated network strength; compare Table 3) calculated from socio-positive behavioral interactions. For display purpose, linear regression lines are depicted.