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Sex/age differences in foraging, vigilance and alertness in a social herbivore

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Abstract

Antipredator strategies and social factors may influence vigilance behaviour in herbivores. Vigilance can differ between sex/age classes, but information is contradictory in the existing literature. We investigated sex/age differences of vigilance in fallow deer *Dama dama*, in a Mediterranean area. Females (> 1 year old) showed a lower proportion of time foraging and a greater alertness rate than males (≥ 1 years old). Decrease of vigilance with increasing group size was observed for females and adult males, but not for young and subadult males, suggesting that group-size effects on vigilance were not consistent across individuals of different sex/age classes. Most likely, females tended to reduce the predation risk for their offspring through a comparatively greater duration and frequency of vigilance. Young/subadult males showed a greater alertness than adult males, which may depend on intraspecific competition in larger groups. Both antipredator and social factors could explain sex/age differences of vigilance in fallow deer.

Keywords Vigilance · Head lift · Antipredator behaviour · Group-size effect · Intraspecific competition · Ungulates

Introduction

Vigilance behaviour tends to increase individual survival and fitness thanks to its primary antipredator function (Pulliam 1973). However, although the fitness generally increases, a compromise may occur between vigilance and other activities, e.g. foraging. Vigilance could reduce the food intake rate (birds: Dukas and Kamil 2000; mammals: Illius and Fitzgibbon 1994), leading to long-term costs such as reduced fecundity and survival (Lima and Dill 1990; Lima 1998; Creel and Christianson 2008). Group-living can provide indirect antipredator benefits, because it usually allows individuals to reduce their time spent in vigilance while still achieving a sufficient food intake (group-size effect, e.g. Caraco 1979; Bertram 1980; Elgar 1989; Childress and Lung 2003; Shorrocks and Cokayne 2005). In addition to the antipredatory function, vigilance may be used to monitor conspecifics (Beauchamp 2015). Individuals may scan to detect and prevent potential attacks from competitors living in the same group (birds: Goss-Custard et al. 1999; mammals: Favreau et al. 2010). Agonistic interactions among conspecifics are driven by dominance hierarchies. In turn, vigilance may also be affected by the rank of competitors (Beauchamp 2015). Dominance is often related to individual features like body size or other phenotypic attributes, which are usually related to age (birds: Searcy and Wingfield 1980; Holberton et al. 1990; mammals: Coltman et al. 2002; Mainguy et al. 2008). Moreover, in polygynous species, males are larger than females, which may imply a lower predation risk (e.g. Main et al. 1996) leading, in turn, to a lower vigilance. Additionally, parental care and offspring protection are important constraints which are expected to influence vigilance behaviour of the sex showing the greatest parental investment, such as females in polygynous species (e.g. Ferretti et al. 2014a). As a result, sex and age are expected to be important factors involved in individual differences of vigilance (Elgar 1989).

In ungulates, vigilance can differ between males and females, but results are not consistent across studies. Some authors observed higher vigilance levels in females than in males (e.g. red deer *Cervus elaphus*: Childress and Lung 2003; roe deer *Capreolus capreolus*: San José et al. 1996; sheep *Ovis aries*: Michelena et al. 2006; Apennine chamois *Rupicapra pyrenaica ornata*: Ferretti et al. 2014a), most likely because of the presence of offspring, which are more vulnerable to predation than adults (e.g. Hunter and Skinner 1998; Childress and Lung 2003). Other studies have reported greater vigilance levels in males than in females (e.g. guanaco *Lama guanicoe*: Marino and Baldi 2008; vicuña *Vicugna vicugna*: Vilá and Cassini 1994; impala *Aepyceros malampus*: Shorrocks and Cokayne 2005; Tibetan gazelle *Procapra picticaudata*: Li and Jang 2008; Przewalski's gazelle *Procapra przewalskii*: Shi et al. 2011; plains zebra *Equus bruchellii*: Simpson et al. 2012). However, many of these studies have been conducted during the mating season, when territorial males, or males holding a harem, are expected to spend long periods watching the females and looking out for rival males (Shorrocks and Cokayne 2005; Lung and Childress 2007). In contrast, other authors have not found significant differences between females and males in the amount of time spent in vigilance (e.g. giraffe *Giraffa camelopardalis*: Cameron and Du Toit 2005).

Group-size effects on vigilance behaviour, if any (e.g. Beauchamp 2001, 2003), may not occur in both sexes (Shorrocks and Cokayne 2005; Lung and Childress 2007; Shi et al. 2011). For example, in males, vigilance may not decrease with increasing group size because they should monitor more competitors for mates and/or food when group is larger (e.g. Shi et al. 2011; Zheng et al. 2013). Establishment of social dominance is common among males of polygynous ungulates (Emlen and Oring 1977; Clutton-Brock et al. 1979; Appleby 1980). As a result, the effect of group size on vigilance could be inconspicuous or even reversed in males, especially subordinate males. Similarly, females could increase vigilance behaviour to limit harassment by conspecific individuals or, in mixed-sex groups, to prevent infanticide (e.g. Pluháček and Bartoš 2000).

Phenology of vigilance behaviour may also be influenced by age of individuals, but previous studies have provided contradictory results. Juveniles may be less vigilant than adults because of greater spatial movements, higher exploratory behaviour and inexperience (e.g. springbok *Antidorcas marupialis*: Bednekoff and Ritter 1994). Other authors have considered the age of an individual as a function of its reproductive status and social rank. Breeding individuals, e.g. territorial or harem-holding adults, could be the most vigilant ones, because they should monitor the presence of possible rivals (e.g. impala: Shorrocks and Cokayne 2005; red deer: Lung and Childress 2007). Conversely, younger individuals could be the most alerted ones, as they should avoid aggression by the more dominant adults (e.g. red deer: Thouless 1990; Apennine chamois: Lovari and Rosta 1985; Przewalski's gazelle: Li et al. 2012). Individuals belonging to different sexes or age classes can be subject to different pressures (e.g. predation or harassment by conspecific, dominant individuals), which would be expected to trigger different vigilance levels or inconsistent responses of vigilance levels to group size variations. In turn, the assessment of vigilance in individuals belonging to different sex/age classes would be important to evaluate specific pressures acting on them (e.g. social or antipredatory).

We investigated variation of feeding and vigilance behaviour in individuals of different sex/age classes, as well as occurrence of group-size effect, in fallow deer *Dama dama*, in autumn-winter, i.e. out of the mating and nursing seasons. We evaluated differences between sexes and, among males, different age classes. We examined different indicators of foraging/vigilance, as they may provide different information (cf. Beauchamp 2008, 2015: 12–13): proportion of time spent feeding and proportion of time spent in vigilance indicate the time allocated in these activities, while vigilance rate indicates the frequency of scans. Our hypothesis was that different sex/age-specific mechanisms underlie vigilance behaviour of fallow deer, i.e. both antipredatory and social (avoidance of harassment by dominant conspecifics) factors. Fallow deer are sexually size dimorphic ungulates (Apollonio 2003), with both sexes usually living in large, unisexual groups (e.g. Thirgood 1996; Apollonio et al. 1998; Ciuti et al. 2008). Females could be expected to be more vulnerable to predation than males, and, in turn, they may show higher vigilance levels than males. Additionally, in autumn/winter, fawns are still in groups with their mother and other females: we could expect that females are more vigilant than males to increase fawn protection. Among males, young and subadult individuals could be predicted to be more vigilant than adults, because of interference from larger/older, thus dominant (Clutton-Brock et al. 1988; McElligot et al. 2001), males. In turn, foraging levels should show the reverse, i.e. feeding should be greater in males than in females, and adult males should spend more time feeding with respect to young and subadult males. One could also expect that group-size effects on foraging and vigilance occur in females and adult males, with an increase in foraging and a decrease in vigilance with increasing group size. Conversely, in subordinates, i.e. young and subadult males, group-size effect would not be expected, because of interference from dominant, adult males in larger groups. We predicted that (i) females would be more vigilant than males of different age classes; (ii) young and subadult males would be more vigilant than adult ones; and (iii) vigilance would decrease with increasing group size in both females and adult males, but there would be no group-size effect in young and subadult males.

Methods

Study area

Our study was conducted in a meadow of the Maremma Regional Park (MRP, Central Italy, 42°39' N, 11°05' E; mid-November–March, 2006–2008 and 2012–2013). The local climate is Mediterranean, with dry summer and wet autumn/winter (mean annual rainfall 670 mm; mean annual temperature 13.2–15.5 °C). Our study area (167.2 ha) included only shrub/grassland (Ferretti et al. 2011a), bordered by Mediterranean scrubwood dominated by holm oak *Quercus ilex*. Wild boar *Sus scrofa* and roe deer also attended the area. Main predators of fallow deer present in MRP during the data collection time were wolf-dog hybrids *Canis lupus* (Manghi and Boitani 2012; Caniglia et al. 2013). Fallow deer and wild boar culling, as well as wild boar captures for population control, occurred in some areas of MRP (Ferretti et al. 2014b; Pecorella et al. 2016), conducted by authorised operators (fallow deer: from October to March) and Park Wardens (both species: throughout the year). Culling did not occur in our study area (Pecorella et al. 2016).

Summer densities of fallow deer were high (36.0–42.1 deer/100 ha, estimated through pellet group counts; Fattorini et al. 2011; Ferretti et al. 2011b; Sforzi et al. 2014). Densities did not differ significantly between periods (2006–2008 vs 2012–2013, Wilcoxon test: $V=6$, $p=0.784$, $n=6$ sampling plots).

Behavioural observations

Behavioural observations were conducted from vantage points, through 10×42 binoculars and 20×60 Leica spotting scopes, by one observer. Data were collected over sessions of 3 h each, at dawn and dusk, 2–5 days/week, between November and mid-March 2006–2008 and 2012–2013, to avoid both the effects of mating (early autumn: Apollonio 2003) and calving (late spring: Apollonio 2003). Activities of fallow deer were recorded using a tape recorder, through focal animal sampling (Lehner 1996), in 10-min bouts/individual. We recorded feeding (the animal grazes or browses, still or in movement), vigilance behaviour (the animal lifts its head above the body axis, intently looking at/around and orienting the ears towards the source of disturbance, if any) and other activities (San José et al. 1996). Before starting each observation bout, we recorded the group size (median \pm inter-quartile range = 16 ± 12 ; mean \pm SE = 18.73 ± 0.69 ; min = 1, max = 73; $N = 525$). A group was defined as the number of individuals at a mutual distance lower than 40 m (Bruno and Lovari 1989). We collected data on different sex/age classes: females (> 1 year old, F), young males (prickets 1 year old, YM), subadult males (sores 2–4 years old, SM), and adult males (bucks > 4 years old, AM); male age classes were estimated considering body size and size/shape of antlers (Apollonio 2003). We found differences neither in mean nor in median group size of the observed (i.e. focal) male and female individuals (male group size: median \pm interquartile range = 15 ± 13 ; mean \pm SE = 18.46 ± 0.86 ; $N = 373$; female group size: median \pm interquartile range = 16 ± 15 ; mean \pm SE = 19.42 ± 1.16 ; $N = 152$; Monte Carlo permutation test for equal means: $p = 0.538$; Mood test for equal medians: $\chi^2 = 1.346$; $p = 0.246$).

We collected data on different individuals within the same day of observation (Frid 1997), as we could temporarily distinguish them by their location and small morphological differences (colour/spot patterns, scars: Marino 2010). Yet, for analyses, we considered only intervals more than 5 min long (Shi et al. 2011).

Statistical analyses

We used generalised linear models (Crawley 2007) to assess the effects of sex/age class and group size on proportion of time spent foraging (PTF), proportion of time in vigilance (PTV) and alertness rate (AR: n. head-lifts/min). PTF and PTV, being continuous variables ranging from 0 to 1, were modelled with beta errors (logit link), while AR, being a continuous, positive variable, was modelled with a gamma distribution (log link). Sex/age classes (cf. above: females; young males; subadult males; adult males), group size and the interaction between these variables were set as predictors. We performed model selection using the ‘dredge’ function in the R package ‘MuMIn’ (Bartoń 2012), to fit all possible models. Model selection used Akaike’s Information Criterion corrected for small sample sizes (AIC_c): Models were retained for inference if they had $\Delta AIC_c \leq 2$ and if their AIC_c value was lower than that of any simpler, nested alternative (Burnham and Anderson 2002). We estimated parameters (coefficients, standard errors and 95% confidence intervals) of the best model, for each response variable, through the ‘glmmadmb’ function in the R package ‘glmmADMB’, version 0.8.3.4 (Bolker et al. 2012). The significance of predictors was assessed by checking whether 95% confidence intervals included 0.

Data availability The dataset analysed during the current study is available from the corresponding author on reasonable request.

Results

Analyses supported an effect of sex on proportion of time spent foraging, PTF (Tables 1 and 2; Fig. 1). Time spent feeding was the lowest in females (mean \pm SE = 0.92 ± 0.01 ; Fig. 1) and the greatest in adult males. In particular, PTF of males tended to increase with age class (young 0.93 ± 0.02 ; subadult 0.94 ± 0.01 ; adult 0.96 ± 0.01 ; Fig. 1).

The time spent in vigilance, PTV, was influenced by the interaction between sex/age classe and group size (Tables 1 and 2; Fig. 1). In particular, PTV tended to decrease with increasing group size, for both females and adult males

Table 1 Effects of sex/age class and group size on proportion of time feeding (PTF), proportion of time in vigilance (PTV) and alertness rate (AR: number of head-lifts/min) in fallow deer, estimated through GLMs. Summaries of selected models are shown

Indicator	Model retained	<i>K</i>	logLik	AICc	ΔAICc	Weight
PTF	Sex/age class	5	4346.62	- 8683.1	0	1
PTV	Sex/age class + group size + sex/age class × group size	9	5571.48	- 11,125.0	0	1
AR	Sex/age class + group size	6	2437.79	- 4863.4	0	0.593
	Sex/age class	5	2436.31	- 4862.5	0.91	0.376

(Table 2; Fig. 2). Conversely, PTV increased with increasing group size for both subadult and young males (Fig. 2).

The alertness rate, AR, was influenced by sex/age class and, to a lesser extent, group size (Tables 1 and 2; Fig. 1; Fig. 2). In particular, AR was the greatest in females (0.31 ± 0.03 head-lifts/min) and decreased with age class in males (young males 0.22 ± 0.04 ; subadult males 0.20 ± 0.03 ; adult males 0.11 ± 0.01).

Discussion

We evaluated how foraging and vigilance behaviour varied in individuals of different sex/age classes, as well as according to group size, in a large herbivore. Our findings showed differences between male and female vigilance, as well as in the occurrence of sex/age-specific group-size effect.

Fallow deer females showed a lower proportion of time foraging, and a greater alertness rate (n. head-lifts/min) than males (our prediction, *i*). We suggest two, not exclusive, explanations to this result. First, sexual differences in vigilance in fallow deer could be explained by sex-related size differences of predation risk (Clutton-Brock et al. 1982). In our study area, preliminary observations suggested that the fallow deer was the main prey of the only large carnivore present, i.e. wolf-dog hybrids (Manghi and Boitani 2012). Sexual size dimorphism is great in fallow deer (Apollonio 2003), with adult males being about 60% larger than females and both sexes tending to stay in large, unisexual groups (e.g. Thirgood 1996; Apollonio et al. 1998; Ciuti et al. 2008). Thus, males may be less vulnerable to predation than females (Clutton-Brock et al. 1982), so females could be more vigilant than males in response to higher predation risk. Second, although fawns were already weaned during the study period, females were still accompanied by offspring, which are the most vulnerable individuals to predation (Childress and Lung 2003). The cost of offspring to mothers is high, not only because of energetic and nutrient demands associated with lactation but also because of constraints associated with the antipredator behaviour that is needed to enhance the protection of young (White and Berger 2001). Presence of offspring can induce females to modify spatial behaviour and habitat selection during the calving season (Ciuti et al. 2006). Offspring are less able to detect a predator and escape from it, so mothers may have to spend more time in vigilance to identify potential predators and escape or hide from them (Clutton-Brock et al. 1982; Hunter and Skinner 1998; Toïgo 1999; Childress and Lung 2003; Lung and Childress 2007; Rieucan and Martin 2008). Females are expected to face a trade-off between food intake and offspring safety (Bunnell and Gillingham 1985). Ungulates are able to scan for predators and process food simultaneously; thus, some of the vigilant time could be used for chewing (Illius and Fitzgibbon 1994). Evaluation of food processing during vigilance would further clarify relationships between foraging and vigilance (e.g. Blanchard and Fritz 2007; Bergvall et al. 2016).

Existing research about group-size effects on vigilance is contradictory (Beauchamp 2001, 2003, 2008). In larger groups, individuals usually reduce vigilance levels because they perceive a lower predation risk (dilution effect and/or detection effect, e.g. Lima 1987; Roberts 1996). In addition, a greater number of potential competitors in large groups could force individuals to invest more time in feeding than in vigilance, to maintain high food intake rates (Beauchamp and Ruxton 2003; but see: Focardi and Pecchioli 2005, for fallow deer). Although we found no effect of increasing group size on time allocated to feeding (see below), both females and adult males decreased their time spent in vigilance while staying in larger groups, which provided support for our prediction (*iii*). Time budget of the observed animals was divided into time spent foraging, time spent in vigilance and time spent in other activities: as proportion of time in vigilance decreased with increasing group size, and time spent foraging did not increase, thus animals may have spent more time in other activities, e.g. social interactions. Although the quantification of agonistic interactions is required to test this hypothesis, this finding could suggest that time saved by the decrease of vigilance was not allocated in foraging, but in social interactions with other individuals, which in turn would have increased with increasing group size. Previous studies showed that vigilance can be affected by intra-group interference (Molvar and Bowyer 1994; Treves 2000;

Favreau et al. 2010), especially in subordinate individuals (i.e. prickets and sores, in fallow deer: Clutton- Brock et al. 1988; McElligot et al. 2001). Accordingly, we observed that young and subadult males spent less time foraging and more time in vigilance, as well as showed greater alertness rates, than adult ones (our prediction, *ii*). We suggest that an increase in vigilance by young/subadult males with increasing group size could depend on intra- specific competition with dominant, adult individuals in large groups (Lung and Childress 2007). Aggressive inter- actions (e.g. sparring, approaches and chases) between males were frequent during behavioural observation, and young males appeared more aggressive than males of other age classes, towards individuals with the same age (I.P., personal observation). High levels of aggression by young males, compared to adult/subadult ones, were also observed towards roe deer, in the same study area (Ferretti 2011). High levels of aggression could determine high levels of vigilance, e.g. to detect and avoid attacks by other young males. In addition, in deer, hierarchy rank is closely related to age, body size and antler size (e.g. Jennings et al. 2006), and adult males are usually dominant over young and subadult ones (Barette and Vandal 1986; Clutton- Brock et al. 1988; McElligot et al. 2001). In particular, prime-age males hold the highest rank (Jennings et al. 2010). Young/subadult males do not have access to mating (Komers et al. 1997; McElligot et al. 1998; McElligot and Hayden 2000), and adult males may preclude them from accessing the best food resources. Indeed, the risk of an attack by adult males (*c.* three times heavier than young ones; Apollonio 2003) could prevent them from decreasing their vigilance levels in large groups.

In conclusion, we suggest that both antipredatory and social factors could explain sex/age differences of vigilance in fallow deer. Most likely, females tended to reduce the predation risk for themselves and offspring through a comparatively greater duration and frequency of vigilance postures than males. In males, social factors, such as competitive interactions and dominance hierarchies in large groups, may explain differences of feeding and vigilance rates among individuals of different age classes. To this end, focusing further research on sex differences in social interactions while telling apart female age classes may help to corroborate the above hypothesis.

Table 2 Best models of proportion of time feeding (PTF), proportion of time in vigilance (PTV) and alertness rate (AR: number of head-lifts/min) in fallow deer, assessed through GLMs. Coefficients (β), standard errors (SEs) and 95% confidence intervals (95% CIs) are shown

Indicator	Predictor	β	SE	95% CI
PTF	Intercept	3.062	0.130	2.807; 3.316
	Sex/age (females)	- 0.628	0.119	- 0.861; - 0.394
	Sex/age (young males)	- 0.435	0.151	- 0.733; - 0.140
	Sex/age (subadult males)	- 0.078	0.120	-0.312; 0.157
PTV	Intercept	- 3.414	0.205	- 3.817; - 3.012
	Sex/age (females)	0.245	0.242	-0.228; 0.718
	Sex/age (young males)	- 0.200	0.151	-0.712; 0.312
	Sex/age (subadult males)	- 0.257	0.213	-0.676; 0.161
	Group size	- 0.024	0.009	- 0.042; - 0.005
	Sex/age class (females) \times group size	0.013	0.012	- 0.011; 0.037
	Sex/age class (young males) \times group size	0.044	0.012	0.020; 0.067
	Sex/age class (subadult males) \times group size	0.026	0.011	0.005; 0.047
AR	Intercept	- 2.084	0.238	- 2.550; - 1.618
	Sex/age (females)	1.132	0.317	0.510; 1.754
	Sex/age (young males)	0.855	0.408	0.055; 1.655
	Sex/age (subadult males)	0.722	0.330	0.075; 1.369
	Group size	- 0.013	0.007	- 0.027; 0.001

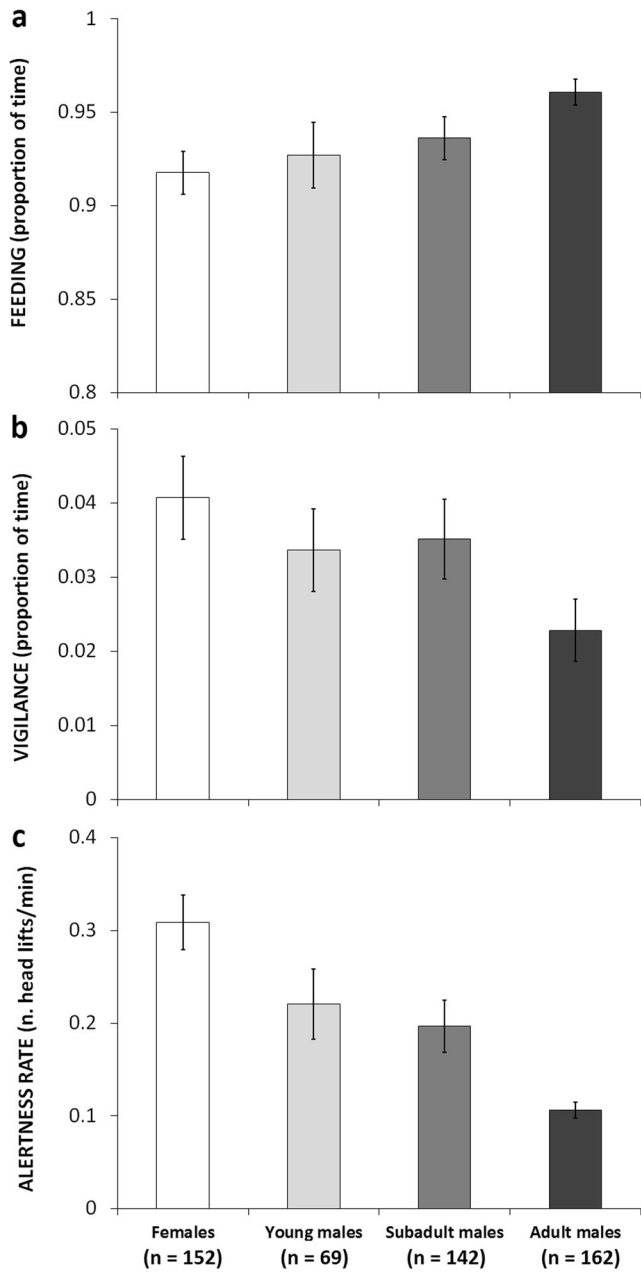


Fig. 1 Mean proportion of time spent feeding (a), mean proportion of time in vigilance (b) and mean alertness rate, i.e. number of head-lifts/min (c), of fallow deer belonging to different sex/age classes. Error bars: standard error

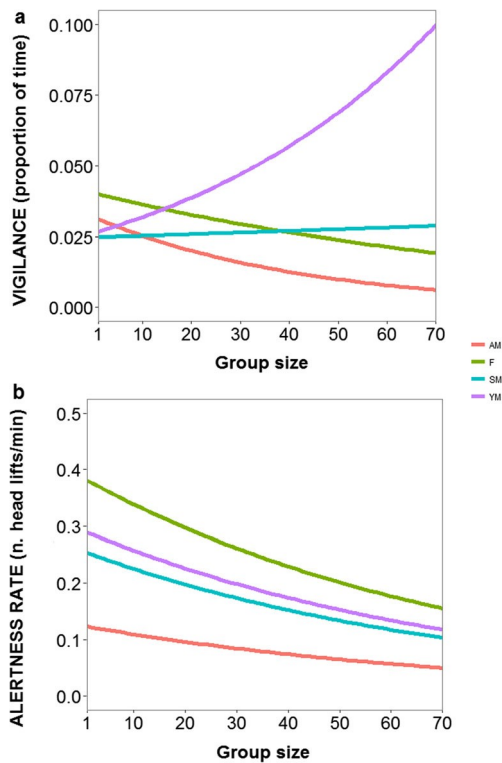


Fig. 2 Relationship between group size and a proportion of time in vigilance and b alertness rate, in each sex/age class. F females, AM adult males, SM subadult males, YM young males

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Author contributions F.F. planned this study, collected data in 2006–2008, performed statistical analyses, supervised all stage of this study and participated in writing up all drafts. I.P. collected data in 2012–2013 and participated in writing up all drafts. N.F. performed statistical analyses and participated in writing up. E.M. participated in data discussion and in writing up.

Compliance with ethical standards

Conflict of interest The authors declare that they have no conflict of interest.

Ethical approval This article does not contain any studies with human participants performed by any of the authors.

Informed consent This article does not contain any studies with human participants.

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