FitzGibbon CD. 1990. Mixed-species grouping in Thomson's and Grant's gazelles. Animal Behaviour:1116-26.

Keywords: 1Afr/1TZ/Acinonyx jubatus/antipredator benefits/cheetah/gazelle/mixed-species group/predator detection/Serengeti National Park

Abstract: Thomson's gazelles and Grant's gazelles in the Serengeti National Park frequently associate in mixed-species groups. Here the antipredator benefits of such associations are investigated. Compared with remaining as a smaller group of conspecifics, joining Grant's gazelles to form larger mixed-species groups had several advantages for Thomson's gazelles. One advantage is that they were less vulnerable to cheetahs, one of their main predators, as a result of improved predator detection, the lower success rate of cheetah hunts and the tendency for cheetahs to avoid hunting larger groups.

Anim. Behav., 1990, **39**, 1116–1126

Mixed-species grouping in Thomson's and Grant's gazelles: the antipredator benefits

CLARE D. FITZGIBBON*
Sub-department of Animal Behaviour, Madingley, Cambridge CB3 8AA, U.K.

Abstract. Thomson's gazelles, *Gazella thomsoni*, and Grant's gazelles, *G. granti*, in the Serengeti National Park, Tanzania, frequently associate in mixed-species groups. Males are more likely to associate than females. Here the antipredator benefits of such associations are investigated. Compared with remaining as a smaller group of conspecifics, joining Grant's gazelles to form larger mixed-species groups had several advantages for Thomson's gazelles. First, they were less vulnerable to cheetahs, *Acinonyx jubatus*, one of their main predators, as a result of improved predator detection, the lower success rate of cheetah hunts and the tendency for cheetahs to avoid hunting larger groups. Second, the Thomson's gazelles in mixed-species groups shared vigilance to some extent with the Grant's gazelles, leaving more time available for feeding. However, compared with joining conspecifics, joining Grant's gazelles to form mixed-species groups had few additional advantages and such associations were likely to be beneficial only when the number of conspecifics in the resulting mixed-species groups was relatively high. Associating with Grant's gazelles did not, for example, enable individual Thomson's gazelles to spend less time vigilant than associating with the same number of conspecifics. Grant's gazelles benefited from the association because the cheetahs' preference for the smaller Thomson's gazelles reduced the rate at which the Grant's gazelles were attacked when in mixed-species groups.

By associating with conspecifics, individuals are frequently considered to benefit from a reduced risk of predation (Neill & Cullen 1974; Kenward 1978; Foster & Treherne 1981; Morgan & Godin 1985). Such antipredator advantages of grouping are thought to arise in two ways. First, predators hunting grouped prey tend to have lower success rates than those hunting singletons (Kenward 1978; Morgan & Godin 1985). This results from the superior ability of groups to detect (Powell 1974; Siegfried & Underhill 1975; Kenward 1978; Lazarus 1979), confuse (Neill & Cullen 1974; Milinski 1977; Pitcher 1986) and mob predators (Hoogland & Sherman 1976; Curio 1978; Shedd 1982; Buitron 1983). Second, as members of groups, individuals have a lower probability of being selected by the predator, as a result of the dilution effect (Hamilton 1971; Bertram 1978a; Foster & Treherne 1981; FitzGibbon 1988). In addition, individuals in groups may also spend less time being vigilant than singletons (Powell 1974; Berger 1978; Caraco 1979; Lazarus 1979; Lipetz & Bekoff 1982), and, as a result, have more time available for feeding (Caraco 1979; Elgar et al. 1986).

*Present address: Institute of Terrestrial Ecology, Monks Wood Experimental Station, Abbots Ripton, Huntingdon, Cambridgeshire PE17 2LS, U.K.

Such benefits of grouping may also accrue to members of mixed-species groups (Morse 1970; Krebs 1973; Barnard et al. 1982; see Barnard & Thompson 1985 for a review). Metcalfe (1984), for example, found that two wader species, turnstones, *Arenaria interpres*, and purple sandpipers, *Calidris maritima*, both shared vigilance with other wader species found in the same habitat. In another study, more vigilant gulls, *Larus ridibundus*, provided lapwings, *Vanellus vanellus*, and golden plovers, *Pluvialis apricaria*, with early warning of predators, partially offsetting the cost of the gulls' kleptoparasitism (Thompson & Barnard 1983). However, individuals can benefit from the early-warning advantage of mixed-species associations only if the information that a predator has been detected is transmitted to participants and if all group members are alert for the same predator species (Leuthold 1977; Metcalfe 1984). An additional benefit of mixed-species grouping may arise if predators show a preference for a particular prey species. Sinclair (1985), for example, suggested that zebra, *Equus burchelli*, in the Serengeti can reduce their risk of predation by staying close to wildebeest, *Connochaetes taurinus*, the preferred prey of large carnivores in the area.

0003–3472/90/061116+11 $03.00/0

Despite considerable interest in the advantages of mixed-species flocking for participants, data are still lacking on two aspects of these associations. First, although many studies have considered predation pressure to be a major force promoting their formation (Gosling 1980; Grieg-Smith 1981; Gautier-Hion et al. 1983; Sullivan 1984), there is little direct evidence that individuals can reduce their risk of predation by associating with heterospecifics. Notable exceptions include studies of 'timid' bird species nesting in the vicinity of 'bold' ones (Clark & Robertson 1979; Dyrcz et al. 1981). Silver grebes, *Podiceps occipitalis*, nesting in brown-hooded gull, *L. maculipennis*, colonies, for example, breed more successfully than those nesting in colonies without gulls (Burger 1984).

Second, most studies have concentrated on the antipredator advantages of mixed-species grouping for bird species, while ungulate associations have received relatively little attention, despite the fact that ungulate species are often found in mixed-species groups (Washburn & De Vore 1961; Altmann & Altmann 1970; Elder & Elder 1970; Leuthold 1977; Gosling 1980; Sinclair 1985). Studies of Thomson's, *Gazella thomsoni*, and Grant's, *G. granti*, gazelles in the Serengeti ecosystem have shown that these two species associate more closely than expected by chance (Bradley 1977; Sinclair 1985). They show a high degree of overlap in their use of habitat and vegetation types (Bradley 1977; Sinclair 1985) and share several common predators, particularly cheetahs, *Acinonyx jubatus*, lions, *Panthera leo*, spotted hyaenas, *Crocuta crocuta*, and wild dogs, *Lycaon pictus* (Estes 1967), despite the fact that Grant's gazelles are rather larger (mean weights of males and females are 60 and 41 kg, respectively) than Thomson's gazelles (25 and 18 kg, Ledger 1968). Their alarm snorts are very similar and each species is reported to react to the snorts and also to the alarm posture of the other (Estes 1967).

My aim in this paper is to determine whether a Thomson's gazelle reduces its vulnerability to predation by associating with Grant's gazelles. In addition, I consider whether the antipredator advantages of joining Grant's gazelles are greater than those of joining conspecifics. Potential advantages that are considered include 'sharing' vigilance with other group members, early-warning of attacks by predators, a reduction in the probability of being the individual selected as the focus of an attack (either as a result of the dilution effect or by associating with a species preferred by predators), and a reduction in the success rate of attacks by predators. Because predators hunting in the wild have a choice of prey groups and are likely to concentrate on the most vulnerable ones, a reduced hunting success against mixed-species groups may also be reflected in a decrease in the number of attacks experienced by mixed-species groups (Caro & FitzGibbon, in press).

METHODS

Thomson's gazelles and one of their main predators, the cheetah, were observed on the long-, intermediate- and short-grass plains of the Serengeti National Park, Tanzania, between March 1985 and April 1987. I spent 1752 h following hunting cheetahs, during which time I collected data on 209 hunts of adult Thomson's gazelles in both single- and mixed-species groups. Observations were made from a Landrover during daylight hours, using 10 × 50 binoculars, and were recorded onto tape for later transcription to data sheets.

Association between the Two Species

To determine the relative frequency of mixed- and single-species Thomson's and Grant's gazelle groups in the study area, I recorded the number of each type of group (single-species Thomson's gazelles, single-species Grant's gazelles or mixed-species groups) that were within 1 km of the vehicle each time I scanned the local area with binoculars while looking for cheetahs over a period of about 3 months.

Vigilance Levels

I compared the vigilance levels of the two gazelle species when in single- and mixed-species groups by selecting a gazelle from a group and recording its vigilance behaviour on a continuously running tape-recorder for 5 min. The data were later transcribed using a stopwatch to measure scan durations to the nearest second and the percentage of time spent vigilant was calculated. A scan was said to have started when the focal gazelle lifted its head above shoulder height and to have finished when the gazelle lowered its head and returned to feeding. Time spent walking, grooming or interacting socially was not included as time spent vigilant. A sample was terminated early if the focal animal left the group (leaving was defined as moving more than 50 m away from the closest group member), lay down or started to ruminate. The presence of predators is known to affect vigilance behaviour in other prey species (Caraco et al. 1980; Lendrem 1983; Sullivan 1984), so I did not collect data if any lions, spotted hyaenas, cheetahs, wild dogs or jackals, *Canis mesomelas* and *C. aureus*, were in sight and a watch was abandoned if any appeared. Sampling was not started for at least 5 min after the car was moved into position, approximately 200 m from the group, in case the gazelles were disturbed by its arrival. I sampled only one gazelle of each species from each group and, since the vigilance levels of gazelles may also be affected by the presence of other ungulate species, only groups that were comprised entirely of gazelles were used.

At the start of each sampling period, the number of conspecific and heterospecific gazelles in the group were recorded and the height of the vegetation around the group was estimated (<10 cm, 10–30 cm or >30 cm). In addition, individuals were categorized as being on the periphery or in the centre of the group. Peripheral individuals had no group members within a semi-circle on one side of them. Every 30 s during the 5-min watch, I estimated the distance from the focal gazelle to its nearest neighbour (to the nearest 1 m unless the distance was greater than 20 m in which case I estimated it to the nearest 5 m) and the 11 records were later averaged to give a mean nearest neighbour distance for the watch. Subsequent analysis showed that a gazelle's position within the group (periphery versus centre) did not affect its vigilance level (FitzGibbon 1988) and this variable is therefore not included in the analysis presented here.

Ability to Detect Predators

I compared the ability of the two gazelle species to detect predators by recording the identity of the first gazelle from a mixed-species group to detect an approaching cheetah. I then compared the number of each species that was the first group member to detect a predator with the number predicted if the ability of the two species to detect predators was equal, calculated from the mean proportion of the two gazelle species in the mixed groups. The distance from the cheetah at which the first group member detected a predator was also estimated, to the nearest 10 m. I regularly checked estimated distances against known distances. A gazelle was said to have been alerted if it fled and/or adopted the stare posture (Walther 1969), whether or not it alarm snorted. To reduce variation resulting from differences in cheetah behaviour, only cases where a single adult non-hunting cheetah walked directly towards the prey group were used. Data from cheetahs that stalked or crouched during the approach were therefore not included in the analysis. Since the distances at which predators are detected are likely to vary according to the species of predator, observations were collected only in response to cheetahs. This predator species was chosen because it appeared from prior observation that gazelles responded immediately they detected the cheetahs whereas they sometimes looked towards other predators, like spotted hyaenas and wild dogs for example, and then returned to feed (Kruuk & Turner 1967).

Gazelles will benefit from the predator-detecting abilities of other species with which they associate only if the information that a predator has been detected is shared between the group members. To determine whether Thomson's gazelles reacted to the stare postures of Grant's gazelles as rapidly as to those of their own species, I recorded the time from the first adult gazelle in a mixed-species group detecting the cheetah and adopting the stare posture to the nearest adult Thomson's gazelle being alerted. Only those cases where the first gazelle to detect a predator did not appear to alarm snort were used, since gazelles are already known to respond to the alarm calls of other ungulate species (usually by increasing their vigilance levels and looking towards the caller and/or the predator). Although the snort can only be heard from less than 100 m away, it is often possible to tell whether a gazelle has snorted by the movement of the nostrils (Walther 1969). Since the delay to detect a predator may depend on the distance between the two gazelles, the distance was estimated at the time when the second gazelle detected the predator.

Selection of Prey Groups by Cheetahs

To test whether the cheetahs preferred to hunt single-species or mixed-species gazelle groups, I compared the number of groups of each type available to the cheetahs with the number of each type hunted. Hunting cheetahs were followed and the size and type (described as single-species Thomson's gazelles, single-species Grant's gazelle or mixed-species) of any group within 1 km was noted every

15 min. If a group that had already been noted was still within 1 km after 15 min, it was not recorded again or on subsequent scans. Which groups the cheetahs actually hunted (defined as stalking, trotting towards, or running at a group) was also noted.

Group Type and Cheetahs' Hunting Success

When a cheetah hunted a gazelle group, the following measures were recorded: the outcome of the hunt (a hunt was deemed successful if the cheetah managed to kill the gazelle), the number of gazelles of each species in the group (individuals were defined as group members if they were within 50 m of each other), the height of the surrounding vegetation (categorized as <10 cm, 10–30 cm or >30 cm), and the distance of the nearest gazelle in the prey group to the cheetah when it initiated its chase. Only hunts of adult gazelles (as defined by Walther 1973) were used in the analysis. I collected data from 209 hunts: these included 155 hunts of Thomson's gazelles in single-species Thomson's gazelle groups and 54 hunts of Thomson's gazelles in mixed-species Grant's/Thomson's gazelle groups.

RESULTS

Association Between the Two Species

The percentage of Thomson's gazelle groups that contained Grant's gazelles was far lower (28·4%, number of groups composed partly or entirely of Thomson's gazelles = 483, of which 137 were mixed-species) than the percentage of Grant's gazelle groups that contained Thomson's gazelles (50·5%, number of groups composed partly or entirely of Grant's gazelles = 271, of which 137 were mixed-species). The tendency of Thomson's gazelles to associate varied between the sexes; mixed-species groups contained a higher percentage of male Thomson's gazelles (35·4% versus 27·4%) than single-species groups did (Mann–Whitney *U*-test, $z = -6{\cdot}12$, $N_1 = 137$, $N_2 = 346$, $P < 0{\cdot}0001$), while the percentage of females was lower in the mixed-species groups (49·0% versus 42·0%; Mann–Whitney *U*-test, $z = -3.53$, $P < 0{\cdot}001$).

The mixed-species groups that cheetahs hunted were, on average, larger ($\bar{X} \pm \text{SE} = 52{\cdot}9 \pm 7{\cdot}3$ gazelles, $N = 54$) than both the single-species Thomson's gazelle groups ($27{\cdot}7 \pm 5.9$, $N = 155$; Mann–Whitney *U*-test, $z = -7{\cdot}13$, $P < 0{\cdot}0001$) and the single-species Grant's gazelle groups ($17{\cdot}0 \pm 6{\cdot}9$, $N = 21$; Mann–Whitney *U*-test, $z = -7{\cdot}92$, $P < 0{\cdot}0001$). The mean number of Thomson's and Grant's gazelles in the mixed-species groups ($N = 54$) was $33{\cdot}4 \pm 5{\cdot}4$ and $19{\cdot}5 \pm 3{\cdot}2$, respectively.

Table I. The results of ANOVAs considering the effects of group type (single- or mixed-species) on the vigilance level of Thomson's and Grant's gazelles in three categories, varying in the number of conspecifics (1–5, 6–20, >20 conspecifics), controlling for the effects of number of conspecific group members, vegetation height, gazelle's sex and nearest-neighbour distance

Number of conspecifics	Thomson's gazelles		Grant's gazelles	
	F-ratio	*df*	*F*-ratio	*df*
1–5	8·58*	1,135	9·12*	1,103
6–20	2·11	1,140	0·14	1,85
>20	10·63**	1,130	0·12	1,87

The *F*-ratio, degrees of freedom and significance level are given for the effect of group type in each case.
*$P < 0{\cdot}01$; **$P < 0{\cdot}001$.

Antipredator Advantages of Mixed-species Groups

Sharing vigilance

To determine whether the presence of heterospecifics affected the vigilance levels of Thomson's and Grant's gazelles, the proportion of time that gazelles of each species spent vigilant in single-species and mixed-species groups were compared. Analysis of variance techniques were used to correct for the number of conspecific group members, the vegetation height, the gazelle's sex, and its nearest neighbour distance: all variables that have been shown to affect the proportion of time spent vigilant by Thomson's gazelles (FitzGibbon 1988). Since the degree to which vigilance is shared is likely to depend on the number of conspecifics in the mixed-species group, the data were considered separately for gazelles in groups with 1–5, 6–20 and more than 20 conspecifics. When compared with remaining as a smaller group of conspecifics, joining gazelles of the other species resulted in a reduction in vigilance for both Thomson's and Grant's gazelles only if there were five or fewer conspecific group members (Table I, Fig. 1a, b). In this situation, both species decreased their vigilance levels to a greater extent when associating with a greater number of heterospecifics (Fig. 2). Thomson's gazelles in mixed-species groups with more than 20

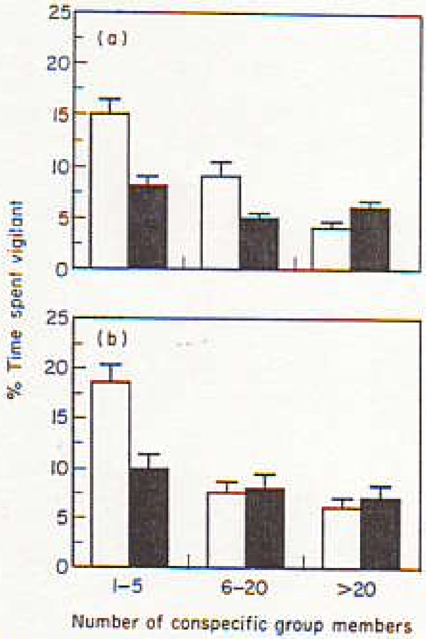

Figure 1. Mean percentage (±SE) of time spent vigilant by (a) Thomson's and (b) Grant's gazelles in single-species (□) and mixed-species (■) groups.

conspecifics actually spent a greater proportion of their time vigilant than they would have done if they had remained as a single-species group (Table I, Fig. 1a). In this situation, vigilance level increased with increasing number of heterospecifics (ANOVA, $F=5{\cdot}56$, $df=3{,}128$, $P<0{\cdot}01$). The results suggest, therefore, that vigilance is shared with heterospecifics only when the number of conspecifics is low.

An additional consideration is whether associating with heterospecifics allows the gazelles to spend less time vigilant than associating with the same number of conspecifics. Vigilance levels of gazelles in mixed-species groups were, therefore, compared with those of conspecifics in single-species groups approximately equal in size to the total group size of the mixed-species group (rather than the number of conspecifics, as done previously). Only in one case, when Thomson's gazelles were in groups with more than 20 conspecifics, did the vigilance levels of gazelles in mixed-species groups differ significantly from those in single-species groups of the same total group size. In this situation, the Thomson's gazelles were more vigilant in the mixed-species groups (Table II).

In summary, the results of this section suggest that the presence of Grant's gazelles in a group tends to have the same effect on the vigilance levels of Thomson's gazelles as does the presence of conspecifics. This appears to be true despite the fact that, on average, Grant's gazelles spend a greater percentage of their time vigilant than Thomson's gazelles ($8{\cdot}7\pm0{\cdot}8\%$ versus $6{\cdot}1\pm0{\cdot}5\%$) when significant effects of total group size, vegetation height, nearest neighbour distance and the gazelle's sex are controlled for (ANOVA, $F=4{\cdot}00$, $df=1{,}338$, $P<0{\cdot}05$).

Improved predator detection

As well as being more vigilant than Thomson's gazelles, Grant's gazelles are also taller. Consequently, they might be expected to have a greater probability of detecting approaching predators and also to detect them at greater distances than Thomson's gazelles. When the number of times that Thomson's and Grant's gazelles were the first group members from mixed-species groups to detect approaching cheetahs (15 and 31 times, respectively) was compared with the number expected if the predator detection abilities of the two gazelle species were equal (31 and 17, respectively), the Grant's gazelles were indeed far more likely to detect predators first ($\chi^2=23{\cdot}41$, $df=1$, $P<0{\cdot}0001$). This was not due to any tendency for Grant's gazelles to congregate on the periphery of mixed-species groups (Grant's gazelles were as likely to be located in the peripheral positions as Thomson's gazelles, $\chi^2=2{\cdot}80$, $df=1$, $N=489$, $P>0{\cdot}10$). Grant's gazelles also detected the cheetahs at greater distances than the Thomson's gazelles (ANOVA, $F=5{\cdot}53$, $df=1{,}248$, $P<0{\cdot}05$), controlling for significant effects of vegetation height ($F=12{\cdot}58$, $df=1{,}248$, $P<0{\cdot}001$) and group size ($F=2{\cdot}79$, $df=4{,}248$, $P<0{\cdot}05$; see Table III for means). It was, therefore, not surprising that mixed-species groups detected approaching cheetahs further away than single-species Thomson's gazelle groups (ANOVA, $F=7{\cdot}40$, $df=1{,}216$, $P<0{\cdot}01$; Table III). They did not, however, detect predators at significantly greater distances than single-species Grant's gazelle groups ($F=2{\cdot}51$, $df=1{,}200$, $P>0{\cdot}10$; Table III). Thus, while the Grant's gazelles provided Thomson's gazelles with early-warning of cheetahs, the Grant's gazelles derived little benefit in this way from the mixed-species association.

Thomson's gazelles will, however, benefit from the early-warning advantage of mixed-species

Number of gazelles	Thomson's gazelles		Grant's gazelles	
	F-ratio	*df*	*F*-ratio	*df*
1–5	0·52	1,90	1·61	1,56
6–20	0·23	1,124	0·15	1,64
>20	15·29*	1,185	0·17	1,148

The *F*-ratio, degrees of freedom and significance level are given for the effect of group type in each case.
$^*P<0{\cdot}001$.

First to detect = Grant's gazelle	206 ± 18	65
First to detect = Thomson's gazelle	175 ± 8	190
Group in high vegetation (≤ 30 cm)	206 ± 10	125
Group in low vegetation (> 30 cm)	162 ± 9	130
When alone	143 ± 12	44
In groups of 2–5 gazelles	170 ± 14	57
In groups of 6–20 gazelles	179 ± 12	60
In groups of 21–50 gazelles	215 ± 19	47
In groups of > 50 gazelles	225 ± 18	47
In mixed-species groups	214 ± 16	48
In single-species Thomson's gazelle groups	173 ± 7	175
In single-species Grant's gazelle groups	190 ± 18	32

grouping only if they are alerted when a Grant's gazelle detects an approaching predator. The two species are known to react to the alarm snorts produced by heterospecific group members, but in many cases the first gazelle to detect a predator only adopts a stare posture (Walther 1969). Where no alarm snort was given, the delay from the first gazelle in a mixed-species group adopting the stare posture to its nearest Thomson's gazelle being alerted was no greater if the first gazelle to detect was a Grant's gazelle ($108{\cdot}6 \pm 17{\cdot}1$ s versus $116{\cdot}5 \pm 42{\cdot}9$ s) than if it was a Thomson's gazelle (ANOVA, $F=1{\cdot}57$, $df=1{,}123$, $P>0{\cdot}20$), when the significant effect of the distance between the two gazelles was taken into account ($F=5{\cdot}25$, $df=1{,}123$ (covariate), $P<0{\cdot}05$; the delay to detect was longer when the distance between the first and second gazelle to detect a predator was greater).

Reduced predator hunting success

When a cheetah hunts an adult Thomson's gazelle, the short, fast chase is usually preceded by a

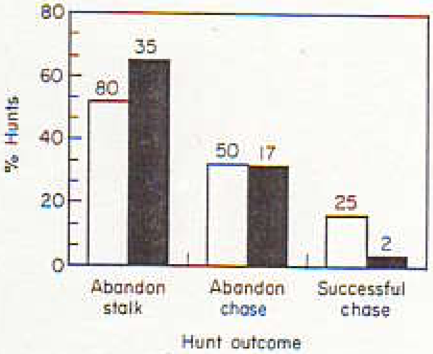

Figure 3. The effect of group type on the outcome of 209 cheetah hunts of Thomson's gazelles. Numbers above the bars refer to sample sizes. □: Single-species groups; ■: mixed-species groups.

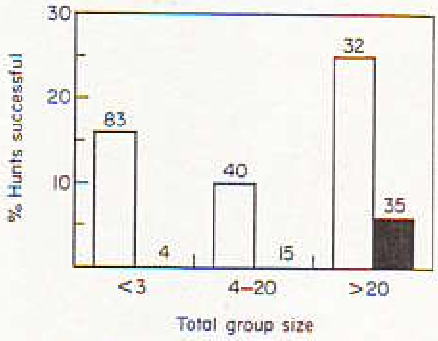

Figure 4. The effects of prey group type and total group size on cheetahs' success at hunting Thomson's gazelles. Numbers above the bars refer to sample sizes. □: Single-species groups; ■: mixed-species groups.

period of stalking when the cheetah attempts to get as close as possible to the prey without being detected. Overall, cheetahs were less successful hunting Thomson's gazelles from mixed-species groups than from single-species groups ($\chi^2=5{\cdot}49$, $df=1$, $P<0{\cdot}05$) and this was partly due to them abandoning a greater proportion of stalking attempts and partly a result of them being less successful at actually chasing gazelles from these groups ($\chi^2=6{\cdot}06$, $df=2$, $P<0{\cdot}05$; Fig. 3). Previous studies of cheetahs have shown that chases started further from the prey are less likely to be successful (Caro 1986). Consequently, a tendency to initiate chases further from mixed-species groups, when compared with single-species Thomson's gazelle groups (58 ± 6 m versus 44 ± 4 m; Mann–Whitney U-test, $z=-2{\cdot}54$, $N_1=19$, $N_2=71$, $P=0{\cdot}01$), was one reason why cheetahs were less successful chasing mixed-species groups.

The lower success rates of cheetahs hunting mixed-species groups were not due to mixed-species groups being found in lower vegetation than single-species groups ($\chi^2=2{\cdot}96$, $df=2$, $P>0{\cdot}10$; cheetahs are less successful stalking their prey in areas with little cover, Eaton 1970). It was also unlikely that it resulted simply from the greater size of mixed-species groups, because cheetahs' hunting success recorded in the wild does not consistently decrease with increasing prey group size (FitzGibbon 1988). To try to control for prey group size, the effect of group type on hunting success was considered separately for groups in three size categories (1–3, 4–20, >20 group members; the boundaries of the categories were chosen so that the number of groups in each category were as similar as possible). Cheetahs appeared to be less successful hunting mixed-species groups in all three group size categories (when the total number of group members exceeded 20, $\chi^2=4{\cdot}89$, $df=1$, $P<0{\cdot}05$) although the number of hunts of mixed-species groups with 20 or fewer group members was too small to allow statistical analysis (Fig. 4).

Reduced attack rate

In the previous section, I have shown that, overall, cheetahs tend to be less successful when hunting Thomson's gazelles that are associated with Grant's gazelles than those in single-species groups. Consequently, cheetahs may prefer to hunt Thomson's gazelle groups rather than mixed-species groups. This possibility was examined by comparing the number of each type of group available to hunting cheetahs with the number of each type that they hunted. The cheetahs hunted a greater proportion of single-species Thomson's gazelle groups that were available to them (34·3%, $N=102$) than mixed-species groups (18·8%, $N=69$, $\chi^2=4{\cdot}92$, $df=1$, $P<0{\cdot}05$). Since cheetahs prefer to hunt small groups containing fewer than 10 gazelles in preference to larger groups (FitzGibbon 1988), and mixed-species groups are, on average, larger than single-species groups (see earlier), cheetahs may prefer to hunt single-species groups because they are smaller, rather than because they do not contain Grant's gazelles. This was borne out by the finding that there was no difference in the cheetahs' preference for mixed- and single-species groups when groups of up to 10 gazelles and more than 10 gazelles were considered separately ($\chi^2=1{\cdot}76$,

Table IV. The effect of prey group type (mixed-species or single-species) on the probability of capture for a particular Thomson's gazelle in a group that comes within 1 km of a hunting cheetah

Group composition	Probability group hunted	Probability particular gazelle selected	Probability a gazelle killed	Probability particular gazelle killed
1TG	0·59*	1·00	0·23*	0·140
10TG	0·55*	0·10	0·10	0·006
10TG 10GG	0·25	0·09	0·06	0·001
20TG	0·25	0·05	0·25	0·003

TG: Thomson's gazelle; GG: Grant's gazelle.
*From FitzGibbon (1988).

$df=1$, $N=74$, $P>0{\cdot}10$ and $\chi^2=0{\cdot}93$, $df=1$, $N=97$, $P>0{\cdot}10$, respectively).

Once cheetahs have selected to hunt a mixed-species group, they have a choice of chasing a Grant's gazelle or a Thomson's gazelle. Comparing the number of times that they chased gazelles of each species (two Grant's and 19 Thomson's gazelles) with the number predicted if they showed no preference (eight and 13, respectively, calculated from the mean proportion of each species in mixed groups), the cheetahs preferred hunting Thomson's gazelles ($\chi^2=7{\cdot}35$, $df=1$, $P<0{\cdot}05$). Consequently, Thomson's gazelles will experience more attacks when in mixed-species groups than expected if the cheetahs showed no preference.

Costs and Benefits

To illustrate the relative costs and benefits of mixed-species grouping for Thomson's gazelles, consider a single Thomson's gazelle faced with the option of joining either a group of nine conspecifics or one with nine conspecifics and 10 Grant's gazelles. Compared with remaining alone, either option reduces the gazelle's risk of predation, but the risk is even lower in the larger mixed-species group than in the smaller Thomson's gazelle group (Table IV). This partly results from the greater size of mixed-species groups (so the cheetah is less likely to choose to hunt the group) and partly from the lower success rates of cheetahs hunting Thomson's gazelles in mixed-species groups. The gazelle's probability of being selected as the focus of the attack does not change significantly by associating with Grant's gazelles, because, in mixed-species groups, the majority (90%) of hunting attempts are directed at Thomson's gazelles anyway.

Even compared with joining a group of Thomson's gazelles equal in size to the total group size of the mixed-species group, the gazelle is still safer in the mixed-species group (Table IV). Although an individual Thomson's gazelle's probability of being selected as the focus of the attack is higher in the mixed-species group, this is outweighed by the lower probability that an attack will be successful.

DISCUSSION

The results of this study indicate that, compared with remaining as a smaller group of conspecifics, joining Grant's gazelles to form larger mixed-species groups has several advantages for Thomson's gazelles. First, they can 'share' vigilance to some extent with the Grant's gazelles, leaving more time available for feeding. Second, the Thomson's gazelles in mixed-species groups gain increased protection from predators through improved predator detection, the lower success rate of cheetah hunts and the tendency for cheetahs to avoid hunting larger groups.

The benefits for Thomson's gazelles of joining Grant's gazelles, rather than the same number of conspecifics, are, however, rather fewer, since the same reduction in vigilance levels and in the probability of the group being attacked occurs when the group size increases through the addition of either conspecifics or heterospecifics. Although the advantages of improved predator detection and reduced cheetahs' hunting success remain, these advantages have to be balanced against the greater probability of being the individual selected as the focus of an attack, which results from the cheetahs' preference for Thomson's gazelles. Cheetahs may prefer Thomson's gazelles because they are smaller and therefore easier to subdue; their lower vigilance levels may also be a contributary factor because cheetahs tend to select less vigilant group members in preference to their more vigilant neighbours (FitzGibbon 1989). For Thomson's gazelles in mixed-species groups with few conspecifics, the high probability of being the individual selected by the attacking cheetah is likely to outweigh the benefit of reduced cheetah hunting success. A Thomson's gazelle with few conspecifics may also suffer a disproportionately high risk of predation for another reason: to reduce the confusing effects of grouped prey, predators often select individuals that differ slightly from other group members (Mueller 1971, 1975; Ohguchi 1978; Landeau & Terborgh 1986). Wolf (1985), for example, showed that coral reef fish were more likely to leave mixed-species groups if the group had fewer conspecifics. Overall, joining a mixed-species group rather than a Thomson's gazelle group of the same total group size, is likely to be beneficial only if the number of conspecifics in the mixed-species group is relatively high.

Hunts of Thomson's gazelles in mixed-species groups were less likely to be successful, not only because the cheetahs were more likely to abandon stalking attempts, but also because they were less successful at chasing gazelles from mixed-species groups (mainly because they started their chases further away from the prey). Both findings are likely to result from the greater predator-detecting abilities of Grant's gazelles in mixed-species groups: being detected by the prey is the main reason why stalking predators such as cheetahs abandon hunting attempts (Schaller 1972; Bertram 1978b; FitzGibbon 1988), while cheetahs initiate chases further from groups that are more likely to detect them, appearing to trade off the chances of stalking closer, but probably being detected, with the probability of attacking successfully from further away (FitzGibbon 1988).

Since males are far more likely than females to associate in mixed-species groups, it appears that the costs and benefits of associating are different for the two sexes. Male Thomson's gazelles are often prevented from joining conspecifics because they need to defend territories; for example, they frequently try to chase away bachelor males that enter the local area (Walther 1978). As a result, increasing their group size by joining heterospecifics confers greater benefits on males than on females. Gosling (1980) also noted that heterospecific ungulate groups in Nairobi National Park, Kenya commonly consisted of a territorial male of one species associated with males or females of another species.

The amount of time an individual devotes to vigilance behaviour tends to reflect its percieved risk of predation (Lima 1987). Consequently, finding that, when compared with associating with the same number of conspecifics, associating with Grant's gazelles did not allow Thomson's gazelles to devote less time to vigilance, suggests that, overall, Grant's gazelles provide no additional protection from predators. This is surprising considering that the Grant's gazelles provide early-warning of predators as a result of their greater height and vigilance levels. In contrast, Byrkjedal & Kalas (1983) found that dunlins, *Calidris alpina*, spent less time vigilant when feeding with golden plovers, which provided them with early warning of danger, than when feeding with conspecifics. Grant's and Thomson's gazelles are vulnerable to the same predators, so it seems unlikely that the Thomson's gazelles did not 'trust' the Grant's gazelles to detect predators for them. In addition, the Thomson's gazelles are alerted whether a Grant's gazelle, on detecting a predator, alarm snorts (Estes 1967), adopts the stare posture (this study) or flees (personal observations). However, unlike the cheetahs considered in this paper, spotted hyaenas and wild dogs, two other important predators of Thomson's gazelles (Borner el al. 1987), do not rely on surprise attacks (Kruuk & Turner 1967; Kruuk 1972; FitzGibbon & Fanshawe 1988) and consequently the fact that Grant's gazelles provide Thomson's gazelles with early-warning of predators may do little to reduce their vulnerability to these two predator species.

A far higher proportion of Grant's gazelle groups are associated with Thomson's gazelles than vice versa. This is not surprising considering that Grant's gazelles are much less common in the park and therefore have fewer opportunities to associate with conspecifics than Thomson's gazelles. In this study I have tended to concentrate on the anti-predator advantages gained by Thomson's gazelles from associating with Grant's gazelles, but have given little consideration to the advantages that Grant's gazelles may gain from such associations. The main benefit is likely to result from the cheetahs' preference for Thomson's gazelles which reduces the number of attacks they experience; when Grant's gazelles are alone and there are no Thomson's gazelles nearby, they receive the full attention of all the cheetahs in the area but, when associated with Thomson's gazelles, the majority of attacks are directed towards the Thomson's gazelles.

Without a detailed analysis of the costs and benefits of mixed-species grouping for all participants, it is not possible to predict what is the dominant factor causing Thomson's and Grant's gazelles to associate. In particular, there may be feeding advantages that I have not considered in this study. Nevertheless, the results presented here do show that, compared with remaining in a smaller group of conspecifics, joining Grant's gazelles to form larger mixed-species groups is beneficial for Thomson's gazelles hunted by cheetahs. Consequently, predation is one factor favouring the formation of mixed-species groups by Thomson's gazelles.

ACKNOWLEDGMENTS

I thank David Babu, Director of Tanzania National Parks, and Bernard Maregesi, Chief Warden, for permission to work in Serengeti National Park and Professor Karim Hirji, Hassan Nkya, and other members of the Serengeti Wildlife Research Institute for their assistance and support. The research was funded by a studentship from the Science and Engineering Research Council. I am very grateful to P. Bateson, G. Beauchamp, T. Caro, J. Fanshawe, L. M. Gosling, C. Packer, and T. Sinclair for their helpful comments on earlier drafts of the manuscript. This is Serengeti Wildlife Research Institute contribution number 448.

REFERENCES

Altmann, S. A. & Altmann, J. 1970. *Baboon Ecology*. Chicago: University of Chicago Press.

Barnard, C. J., Thompson, D. B. A. & Stephens, H. 1982. Time budgets, feeding efficiency and flock dynamics in flocks of lapwings, golden plovers and gulls. *Behaviour*, **80**, 44–69.

Barnard, C. J. & Thompson D. B. A. 1985. *Gulls and Plovers: the Ecology of Mixed Species Feeding Groups*. London: Croom Helm.

Berger, J. 1978. Group size, foraging and antipredator ploys: an analysis of bighorn sheep decisions. *Behav. Ecol. Sociobiol.*, **4**, 91–99.

Bertram, B. C. R. 1978a. Living in groups: predators and prey. In: *Behavioural Ecology: an Evolutionary Approach* (Ed. by J. R. Krebs & N. B. Davies), pp. 64–96. Oxford: Blackwell.

Bertram, B. C. R. 1978b. *Pride of Lions*. London: J. M. Dent.

Borner, M., FitzGibbon, C. D., Borner, Mo., Caro, T. M., Lindsay, W. K., Collins, D. A. & Holt, M. E. 1987. The decline in the Serengeti Thomson's gazelle population. *Oecologia (Berl.)*, **73**, 32–40.

Bradley, R. M. 1977. Aspects of the ecology of Thomson's gazelle in the Serengeti National Park, Tanzania. Ph.D. thesis, Texas A & M University.

Buitron, D. 1983. Variability in the responses of black-billed magpies to natural predators. *Behaviour*, **87**, 209–236.

Burger, J. 1984. Grebes nesting in gull colonies: protective associations and early warning. *Am. Nat.*, **123**, 327–337.

Byrkjedal, I. & Kalas, J. A. 1983. Plover's page turns into plover's parasite: a look at the dunlin/golden plover association. *Ornis fenn.*, **60**, 10–15.

Caraco, T. 1979. Time budgeting and group size: a test of a theory. *Ecology*, **60**, 618–627.

Caraco, T., Martindale, S. & Pulliam, H. R. 1980. Avian flocking in the presence of a predator. *Nature, Lond.*, **285**, 400–401.

Caro, T. M. 1986. The functions of stotting in Thomson's gazelles: some tests of the predictions. *Anim. Behav.*, 663–684.

Caro, T. M. & FitzGibbon, C. D. In press. Large carnivores and their prey: the quick and the dead. In: *Natural Enemies: the Population Biology of Predators, Parasites and Diseases* (Ed. by M. J. Crawley). Oxford: Blackwell Scientific Publications.

Clark, K. L. & Robertson, R. L. 1979. Spatial and temporal multi-species nesting aggegations in birds as anti-parasite and anti-predator defenses. *Behav. Ecol. Sociobiol.*, **5**, 359–371.

Curio, E. 1978. The adaptive significance of avian mobbing. I. Teleonomic hypotheses and predictions. *Z. Tierpsychol.*, **48**, 175–183.

Dyrcz, A., Witkowski, J. & Okulewicz, J. 1981. Nesting of 'timid' waders in the vicinity of 'bold' ones as an anti-predator adaption. *Ibis*, **123**, 542–545.

Eaton, R. 1970. Hunting behavior of the cheetah. *J. Wildl. Mgmt*, **34**, 56–67.

Elder, W. H. & Elder, N. L. 1970. Social groupings and primate associations of the bushbuck (*Tragelaphus scriptus*). *Mammalia*, **34**, 356–362.

Elgar, M. A., McKay, H. & Woon, P. 1986. Scanning, pecking and alarm flights in house sparrows. *Anim. Behav.*, **34**, 1892–1894.

Estes, R. D. 1967. The comparative behaviour of Grant's and Thomson's gazelle. *J. Mammal.*, **48**, 189–209.

FitzGibbon, C. D. 1988. The antipredator behaviour of Thomson's gazelles. Ph.D. thesis, University of Cambridge.

FitzGibbon, C. D. 1989. A cost to individuals with reduced vigilance in groups of Thomson's gazelles hunted by cheetahs. *Anim. Behav.*, **37**, 508–510.

FitzGibbon, C. D. & Fanshawe, J. H. 1988. Stotting in Thomson's gazelles: an honest signal of condition. *Behav. Ecol. Sociobiol.*, **23**, 69–74.

Foster, W. A. & Treherne, H. E. 1981. Evidence for the dilution effect in the selfish herd from fish predation on a marine insect. *Nature, Lond.*, **293**, 466–467.

Gautier-Hion, A., Quris, R. & Gautier, J. 1983. Monospecific versus polyspecific life: a comparative study of foraging and antipredator tactics in a community of *Cercopithicus* monkeys. *Behav. Ecol. Sociobiol.*, **12**, 325–335.

Gosling, L. M. 1980. Defence guilds of savannah ungulates as a context for scent communication. *Symp. zool. Soc. Lond.*, **45**, 195–212.

Greig-Smith, P. W. 1981. The role of alarm responses in the formation of mixed-species flocks of heathland birds. *Behav. Ecol. Sociobiol.*, **8**, 7–10.

Hamilton, W. D. 1971. Geometry for the selfish herd. *J. theor. Biol.*, **31**, 295–311.

Hoogland, J. L. & Sherman, P. W. 1976. Advantages and disadvantages of bank swallow (*Riparia riparia*) coloniality. *Ecol. Monogr.*, **46**, 33–58.

Kenward, R. E. 1978. Hawks and doves: factors affecting success and selection in goshawk attacks on woodpigeons. *J. Anim. Ecol.*, **47**, 449–460.

Krebs, J. R. 1973. Social learning and the significance of mixed-species flocks of chickadees (*Parus* spp). *Can. J. Zool.*, **51**, 1275–1288.

Kruuk, H. & Turner, M. 1967. Comparative notes on predation by lion, leopard, cheetah and wild dog in the Serengeti area East Africa. *Mammalia*, **31**, 1–27.

Kruuk, H. 1972. *The Spotted Hyena: a Study of Predation and Social Behavior*. Chicago: University of Chicago Press.

Landeau, L. & Terborgh, J. 1986. Oddity and the 'confusion effect' in predation. *Anim. Behav.*, **34**, 1372–1380.

Lazarus, J. 1979. The early warning function of flocking in birds: an experimental study with captive quelea. *Anim. Behav.*, **27**, 855–865.

Ledger, M. P. 1968. Body composition as a basis for a comparative study of some East African mammals. *Symp. zool. Soc. Lond.*, **21**, 289–310.

Lendrem, D. W. 1983. Predation risk and vigilance in the blue tit (*Parus caeruleus*). *Behav. Ecol. Sociobiol.*, **14**, 9–13.

Leuthold, W. 1977. *African Ungulates: a Comparative Review of their Ethology and Behavioral Ecology*. New York: Springer-Verlag.

Lima, S. L. 1987. Vigilance while feeding and its relation to the risk of predation. *J. theor. Biol.*, **124**, 303–316.

Lipetz, V. E. & Bekoff, M. 1982. Group size and vigilance in pronghorns. *Z. Tierpsychol.*, **58**, 203–216.

Metcalfe, N. B. 1984. The effects of mixed-species flocking on the vigilance of shorebirds: who do they trust? *Anim. Behav.*, **32**, 986–993.

Milinski, M. 1977. Experiments on the selection by predators against spatial oddity of their prey. *Z. Tierpsychol.*, **43**, 311–325.

Morgan, M. J. & Godin, J.-G. J. 1985. Antipredator benefits of schooling behaviour in a cyprinodontid fish, the banded killifish (*Fundulus diaphanus*). *Z. Tierpsychol.*, **70**, 236–246.

Morse, D. H. 1970. Ecological aspects of some mixed-species foraging flocks. *Ecol. Monogr.*, **40**, 119–168.

Mueller, H. C. 1971. Oddity and specific searching image more important than conspicuousness in prey selection. *Nature, Lond.*, **233**, 345–346.

Mueller, H. C. 1975. Hawks select odd prey. *Science*, **188**, 953–954.

Neill, S. R. & Cullen, J. M. 1974. Experiments on whether schooling by their prey affects the hunting behaviour of cephalopod fish predators. *J. Zool., Lond.*, **172**, 549–569.

Ohguchi, O. 1978. Experiments on the selection against colour oddity of water fleas by three-spined sticklebacks. *Z. Tierpsychol.*, **47**, 254–267.

Pitcher, T. J. 1986. Functions of shoaling behaviour in teleosts. In: *The Behaviour of Teleost Fishes* (Ed. by T. Pitcher), pp. 294–337. Beckenham: Croom Helm.

Powell, G. V. N. 1974. Experimental analysis of the social value of flocking by starlings (*Sturnus vulgaris*) in relation to predation and foraging. *Anim. Behav.*, **22**, 501–505.

Schaller, G. B. 1972. *The Serengeti Lion: a Study of Predator–Prey Relations*. Chicago: University of Chicago Press.

Shedd, D. H. 1982. Seasonal variation and function of mobbing and related behaviours of the American robin (*Turdus migratorius*). *Auk*, **99**, 342–346.

Siegfried, W. R. & Underhill, L. G. 1975. Flocking as an anti-predator strategy in doves. *Anim. Behav.*, **23**, 504–508.

Sinclair, A. R. E. 1985. Does interspecific competition or predation shape the African ungulate community? *J. Anim. Ecol.*, **54**, 899–918.

Sullivan, K. A. 1984. Information exploitation by downy woodpeckers in mixed-species flocks. *Behaviour*, **91**, 294–311.

Thompson, D. B. A. & Barnard, C. J. 1983. Antipredator responses in mixed-species associations of lapwings, golden plovers and black-headed gulls. *Anim. Behav.*, **31**, 585–593.

Walther, F. 1969. Flight and avoidance of predators in Thomson's gazelle (*Gazella thomsoni* Guenther 1884). *Behaviour*, **34**, 184–221.

Walther, F. R. 1973. On age class recognition and individual identification of Thomson's gazelle in the field. *J. S. Afr. Wildl. Mgmt Ass.*, **2**, 9–15.

Walther, F. R. 1978. Forms of aggression in Thomson's gazelles: their situational motivation and their relative frequency in different sex, age and social classes. *Z. Tierpsychol.*, **47**, 113–172.

Washburn, S. L. & De Vore, I. 1961. The social life of baboons. *Scient. Am.*, **204**, 62–71.

Wolf, N. G. 1985. Odd fish abandon mixed-species groups when threatened. *Behav. Ecol. Sociobiol.*, **17**, 47–52.

(Received 6 March 1989; initial acceptance 12 May 1989; final acceptance 19 June 1989; MS. number: 3367)