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Abstract: A number of studies have shown that prey animals tend to reduce the amount of time they spend vigilant when associated with conspecifics. The effects of individual vigilance levels on the vulnerability of Thomson's gazelles was investigated in the Serengeti National Park, Tanzania. Cheetahs are there the main predator of the Thomson's gazelle, killing approximately 8% of the adult population each year.

**Table I.** The number of birds in each group that derived their songs from either the father, second tutor, both, or neither adult

| Group | Number of birds which learnt from | | | |
|---|---|---|---|---|
| | Father | Tutor | Both | Neither |
| 1 ($N=11$) | 0 | 10 | 1 | 0 |
| 2 ($N=7$) | 3 | 4 | 0 | 0 |
| 3 ($N=8$) | 4 | 0 | 0 | 4 |

here suggest that visual isolation, especially if vocal interaction is also disallowed, allows the young birds to go through the normal song development but is inadequate for song elements that are heard to be used. Instead, the young birds use elements learnt from the father before independence rather than using call notes as song elements, even though they can hear these from the tutor, his mate and their siblings. This demonstrates that young birds do learn at this earlier stage even though they do not normally produce song elements heard then. The availability of a second tutor after independence, with which they have both visual and vocal contact, appears to override this earlier experience. Lack of visual contact also affects accuracy: there was a great difference between group 1, in which song elements were learnt very precisely, and groups 2 and 3, in which song copying was quite poor and not all the elements could be attributed to one or other of the tutors.

The results of these experiments fit in with those of Böhner (1986). He found that young birds isolated from the father at independence, and then maintained in vocal but not visual contact with adults, develop a song based on that of the father. It can be concluded, therefore, that visual and vocal interaction between young zebra finches and their song tutor is important for the timing and accuracy of song learning. While song development proceeds at the normal time without such interaction, elements heard at this stage are not incorporated into song.

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## A Cost to Individuals with Reduced Vigilance in Groups of Thomson's Gazelles Hunted by Cheetahs

A number of studies have shown that prey animals tend to reduce the amount of time they spend vigilant when associated with conspecifics (Powell 1974; Berger 1978; Caraco 1979; Barnard 1980; Elgar & Catterall 1981). The optimal scan rate for an individual in a group will depend, however, on the scan rates of other group members (Pulliam et al. 1982). While selection might be expected to favour those individuals that spend less time scanning than their associates and that, therefore, have more time to feed, such benefits are likely to be offset by increased vulnerability to predators. In this paper I investigate the effects of individual vigilance levels on the vulnerability of Thomson's gazelles, *Gazella thomsoni*, to predation by cheetahs, *Acinonyx jubatus*. In the Serengeti National Park, Tanzania, where my study was carried out, cheetahs are the principal predators of Thomson's gazelles (Schaller 1972), killing approximately 8% of the adult population each year (calculated from Borner et al. 1987). They stalk their prey, generally manoeuvring to within 30 m of the selected victim

before initiating short, fast chases which are usually less than 300 m in length (Schaller 1967). During their concealed approaches they have ample opportunity to assess the vigilance levels of potential prey.

To compare the vigilance behaviour of Thomson's gazelles selected by cheetahs with that of their fellow group members apparently ignored although similarly positioned, the vigilance behaviour of the two individuals nearest to each cheetah at the start of its stalk was recorded. This was done because preliminary observations had suggested that cheetahs tended to select individuals at the edge of a group, usually on the side from which they were approaching. Matching the availability of the two focal gazelles was achieved by using only occasions when the two individuals nearest to the cheetah were adults of the same sex, were nearest neighbours within 5 m of one another and were both on the edge. Cases in which one gazelle was positioned between the cheetah and the other gazelle were also excluded from the analysis. In addition, only actively feeding individuals were observed, although, on four occasions, gazelles that had been feeding at the start of data collection began to ruminate, maintaining the head up posture for the rest of the sampling period. Scanning behaviour of the two gazelles was recorded during the entire stalk (mean duration of stalks $\pm$ SD $= 18{\cdot}6 \pm 4{\cdot}1$ min), starting when the cheetah first adopted the characteristic stalk posture (head low, legs bent) and ending when it initiated its chase. A scan started when the gazelle lifted its head above shoulder level and ended when it returned to feed (i.e. it included time spent ruminating). The percentage of time spent scanning by each individual was later calculated. This measure was chosen in preference to the rate of scanning, commonly used in vigilance studies, because Thomson's gazelles adjust both their rate of scanning and their average scan duration when altering their level of vigilance behaviour (FitzGibbon 1988). If either gazelle detected the stalking predator, as distinguished by the stare posture (Walther 1969), or if the stalk lasted less than 5 min, meaning insufficient data had been collected, the record was not included in the analysis. On the 16 occasions when all these conditions were satisfied the median group size of the gazelles was 8·0 (range 2–30).

On 14 out of the 16 occasions (87·5%), the cheetah chased the less vigilant gazelle of the pair, significantly more often than expected by chance (binomial test, two-tailed, $P = 0{\cdot}004$, Table I). A similar result was found even when the four cases where focal animals started to ruminate, keeping their heads up for the rest of the stalk, were excluded from the analysis (least vigilant chosen on 10 out of 12 occasions, binomial tests, two-tailed, $P < 0{\cdot}038$). Thus, cheetahs do appear to be selecting individuals with lower vigilance levels than their neighbours. The possibility that they were merely chasing the gazelles that were the last to run away was unlikely. Cheetahs appeared to select their prey before initiating chases, moving towards the chosen animal during the last part of the stalk and, having broken cover, continued to chase the same gazelle, irrespective of whether it was the first to run away or not.

**Table I.** The vigilance level (percentage of time spent scanning) and sex of 16 adult gazelles which were chosen by cheetahs compared with their nearest neighbour in the group

| Gazelle chased | | Gazelle ignored | |
|---|---|---|---|
| Vigilance | Sex | Vigilance | Sex |
| 8·0 | Male | 17·5 | Male |
| 31·4 | Male | 63·0 | Male |
| 40·0 | Male | 70·2 | Male |
| 15·7 | Male | 38·8 | Male |
| 40·0 | Male | 45·0 | Male |
| 35·3 | Male | 39·1 | Male |
| 31·7 | Male | 65·2 | Male |
| 68·5 | Male | 72·5 | Male |
| 10·0 | Female | 65·0 | Female |
| 78·7 | Female | 84·2 | Female |
| 52·0 | Female | 50·0 | Female |
| 23·9 | Female | 20·5 | Female |
| 81·0 | Male | 96·3 | Male* |
| 49·7 | Male | 90·1 | Male* |
| 62·0 | Male | 88·3 | Male* |
| 72·6 | Male | 89·9 | Male* |

* Individuals which started to ruminate, maintaining the head up posture during the rest of the stalk.

By selecting the less vigilant animals, cheetahs are expected to increase their probability of making a successful kill. Some evidence for this comes from data on hunts of single gazelles. In these cases, gazelles that the cheetahs were able to catch were, on average, less vigilant during the stalk (mean percentage of time spent vigilant $\pm$ SE $= 43{\cdot}3 \pm 15{\cdot}0$) than those that could not be caught ($76{\cdot}5 \pm 5{\cdot}1$; $t = 2{\cdot}47$, $N = 40,9$, $P < 0{\cdot}05$).

Less vigilant gazelles may be easier to catch and therefore preferred by the cheetahs for two reasons. First, they may be slower to react when the final chase is initiated than more vigilant animals. This is supported by the finding that, for hunts of single gazelles, there was a negative correlation between a gazelle's vigilance level and its delay to flee when

the cheetah initiated the chase ($r = -0{\cdot}394$, $N = 21$, $P < 0{\cdot}05$). In addition, single gazelles that reacted quickly were more likely to escape than those that delayed their flight, comparing the time from when the cheetah initiates its chase to when the prey flees for successful ($\bar{X} \pm \text{SE} = 0{\cdot}8 \pm 0{\cdot}4$ s) and unsuccessful chases ($2{\cdot}0 \pm 0{\cdot}5$ s; $t = 2{\cdot}21$, $N = 14{,}8$, $P < 0{\cdot}05$). The second reason why less vigilant gazelles are easier to catch may be that such individuals are in poor physical condition and unable to run as fast as gazelles in better condition. Animals facing starvation are expected to maximize energy intake by increasing the proportion of time they spend feeding, at the expense of other activities, in particular vigilance. However, the less vigilant gazelles were at a disadvantage irrespective of any differences in their running speeds: when compared with more vigilant animals, such individuals were less likely to have their heads up when the cheetah initiated its chase ($t = 3{\cdot}02$, $df = 6{,}14$, $P = 0{\cdot}01$, comparing the vigilance levels of gazelles that were feeding and those that were looking around, $\bar{X} + \text{SE} = 21{\cdot}0 \pm 9{\cdot}1\%$ and $61{\cdot}1 \pm 8{\cdot}5\%$, respectively) and single gazelles that had their heads up reacted more quickly to the cheetahs than those that were feeding ($t = 2{\cdot}85$, $N = 7{,}14$, $P < 0{\cdot}05$, $\bar{X} \pm \text{SE} = 2{\cdot}1 \pm 0{\cdot}3$ s and $0{\cdot}9 \pm 0{\cdot}4$ s, respectively).

Thus, more vigilant gazelles were less vulnerable to predation because they tended to react more rapidly when the cheetahs started their final rush towards the prey group. Gazelles with the highest vigilance levels in the group may also increase their survivorship through improved predator detection before chases are initiated. A hunt was often abandoned if a gazelle in the prey group detected the cheetah during its stalk (they abandoned on 52 out of 70 hunts when this occurred, 74·3%). If the cheetah continued to hunt and not all the group had detected it by the time it came to chase, it usually selected one of the gazelles that had not yet detected it (on eight out of nine occasions). As a result, the gazelles detecting the predators, which were presumed to be the most vigilant group members, were less likely to be hunted. Previous studies of group vigilance behaviour have assumed that the individual detecting a predator alerts all other group members and as a result there is no benefit to being the first in the group to detect the predator. Clearly this is not the case here, and on the occasions that the first gazelle to detect the cheetah does not signal the alarm, other group members may be alerted only when they notice its stare posture or when it flees. Consequently, scanning behaviour in this species also serves to monitor the alert behaviour of other group members.

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## Early Auditory Learning and Song Improvisation in Nightingales, *Luscinia megarhynchos*

Birds generally acquire songs by imitation, and many species are renowned for their ability to