Induced or routine vigilance while foraging

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Vigilance is time-consuming and, since time is usually a limited resource for free-ranging animals, it may conflict with other activities such as feeding. For several taxonomic groups, however, some authors have questioned the importance of this historical tradeoff (Arenz and Leger 1997, Lima and Bednekoff 1999, Guillemain et al. 2001). Illius and Fitzgibbon (1994) proposed that when food intake rate is limited by chewing and swallowing rates (i.e. process 3 in Spalinger and Hobbs 1992), rather than by food encounter rate (i.e. process 1 or 2 in Spalinger and Hobbs 1992), the remaining ''spare time'' (i.e. the time spent chewing after detection of the next bite) can be used by foragers for other activities, such as vigilance, without reducing the rate of food intake. However, vigilance is shaped not only by the ingestion process (cropping, chewing and swallowing), but also by stimuli of elevated predation risk. Hence, vigilance behaviour is expected to have two components: ''routine vigilance'' when the animal is simply monitoring its surroundings during spare time or ''induced vigilance'' when responding to a stimulus. The scarcity of studies stating the importance of sudden stimuli in vigilance behaviour is puzzling (Lima and Bednekoff 1999, Ruxton and Roberts 1999, Fortin et al. 2004a, Bednekoff and Lima 2005). In addition to the conceptual importance of a distinction between induced and routine vigilance, we believe that this gap in the current research on vigilance behaviour may strongly influence our understanding of the tradeoff between foraging and vigilance.

Clearly, routine vigilance is closely related to the typical form of vigilance fitting both the assumptions and predictions of theoretical models (Illius and Fitzgibbon 1994, Fortin et al. 2004a, 2004b). When foraging on patches of high biomass (i.e. handling-limited foraging, process 3 in Spalinger and Hobbs 1992), animals that can handle food while in the act of

vigilance (i.e. head raised), have the opportunity to scan their surroundings while chewing the current bite before cropping the next (Illius and Fitzgibbon 1994, Cowlishaw et al. 2004, Fortin et al. 2004a). Fortin et al. (2004a) reported that bite size sometimes exceeded mouth dimensions, so that foragers could be vigilant while vegetation gradually entered their mouth. In these situations, foragers are able to match scanning with spare time, thereby allowing for the continuity of the ingestion process, so that vigilance appears to be largely cost-free (Illius and Fitzgibbon 1994, Fortin et al. 2004a).

Unlike routine vigilance where animals can match with precision the particular ingestion process and scanning behaviour, induced vigilance may disrupt the ingestion process since it requires animals to react to unpredictable stimuli whatever the phase of feeding. Accordingly, Fortin et al. (2004a) reported that the proportion of foraging time spent by free ranging elk, *Cervus canadensis,* and bison, *Bison bison,* scanning their surroundings was only a small fraction of the spare time available to them. The negative impact of induced scanning on intake rate is even more important when the stimulus occurs just after an animal has swallowed. In such instances, foragers have nothing to chew while scanning. Moreover, animals engaged in induced vigilance should reduce chewing considerably, even with a mouthful of food. One major reason for animals to reduce chewing when responding to a threat stimulus is because chewing is noisy (so much so that some authors have deployed audio transmitters on animals in order to record bite/chew rates, Laca and Wallis De Vries 2000, Logan and Sanson 2002) and thus may impede a prey's ability to evaluate the level of predation risk. Moreover, the acoustic signals generated by chewing are primarily transmitted by bone conduction and so our own mastication sounds can appear much

stronger than background noise (Amft et al. 2005). Molinari-Jobin et al. (2004) reported that a large proportion (58%) of females roe deer, *Capreolus capreolus,* were killed by lynx, *Lynx lynx,* while ruminating. The authors interpreted this result as being a consequence of impaired hearing. In addition, chewing may also impact on the stabilization of the visual field. Although no study has explicitly investigated this aspect to our knowledge, considering that visual detection might be easier with the head motionless is quite appealing. We thus expect the assumption for cost-free vigilance behaviour (i.e. animals can be vigilant while chewing) to be weak in the case of induced vigilance, a hypothesis on which we focus in this paper.

We believe that distinguishing between the two types of vigilance is needed to improve conceptualization of the relationship between vigilance and foraging. We predict that animals engaged in routine vigilance behaviour chew throughout the vigilance bout, whereas animals engaged in induced vigilance do not, thereby disrupting the ingestion process. In order to test this prediction, we performed a simple experiment on free-ranging impalas, *Aepyceros melampus,* between 5 July and 14 August 2005 in Hwange National Park, Zimbabwe (19°00′S, 26°30′E). We used a digital video camera to record vigilance bouts, defined as: (1) routine vigilance when no apparent stimulus induced scanning behaviour by the focal animals, and (2) induced vigilance when the animals were experimentally alarmed. We induced scanning behaviour by playing a 2.40 s record of two short lion roars (recorded in HNP by WildCRU, Oxford Univ.), from an open-top car parked 60–110 m from the focal impala. Impalas were habituated to cars, and easy to observe. First, we randomly chose a feeding individual, and began to film. We then randomly (and exclusively) assigned this individual to one or the other treatment: experimentally induced (i.e. when the tape was played – about 10 s after the beginning of the recording), or control (i.e. routine) vigilance. We stopped filming once the first vigilance bout (either obtained after the play back or non-induced) was recorded (mean vigilance bout duration: 7.6 s).

Several studies have reported effects of reproductive status, sex, age or group size on vigilance patterns (Quenette 1990). At that time of the year, young are weaned so that there were no differences in reproductive status that may have interfered with our results. To avoid the confounding effects of sex or age, we focused on adult females, the most numerous sex-age class in the group (63 adult females, unpubl.). In addition, we recorded the number of impalas present in the group. As the herd was always relatively compact, the definition of the group was easy. The presence of other species may also affect vigilance behaviour (Scheel

1993), but during this experiment only impalas were observed in the area.

Forage characteristics also affect vigilance patterns (Fortin et al. 2004a). However, all our observations were performed in the same 50×50 m spot, where impalas were often seen grazing mostly on a single type of food (couch grass, *Cynodon dactylon*). Moreover, the grass patch was watered by regular overflows from the nearby waterhole, and thus remained green and regularly used during the whole period (and thus kept at short height by grazing). Therefore, although we did not measure vegetative characteristics, we assumed that changes in quality and quantity of resources were not an issue in our experiment.

Because we wanted to investigate the tradeoffs between vigilance and foraging, we focused on cases where theoretical models predict cost-free vigilance behaviour i.e. when the instantaneous intake rate of the forager is locally limited by handling time rather than by encounter rate (Illius and Fitzgibbon 1994). We considered an animal to meet this assumption when it fed at the same place before and after a vigilance bout, i.e. at the scale of the feeding station (Bailey et al. 1996). Overall we considered 17 induced and 22 routine vigilance bouts. We evaluated 6 behavioural variables: (1) the head lifting duration; (2) the time lag before the first chew once the neck was erected; (3) the total number of chews during a vigilance bout; (4) the total duration of the vigilance bout (i.e. time lag between the beginning of the head lift and the end of the head descent); (5) the chew frequency while vigilant (i.e. (3)/(4)) and (6) the chew frequency while chewing. Since the impalas considered in this experiment were not individually recognizable, we may have observed the same animal more than once, although never on the same day. These probably rare cases of multiple observations of the same animal under different conditions are not likely to bias our conclusions from the statistical analyses on the qualitative difference between routine and induced vigilance, as results are clear and highly significant.

Animals in routine and induced vigilance strongly differed in scanning patterns. An animal experimentally alarmed raised its head faster (Mann–Whitney $U_{22,17} = 101$, $p = 0.01$; Fig. 1a) and subsequently chewed less, both in total (Mann–Whitney $U_{22,17} = 90$, $p = 0.005$; Fig. 1b) and per second of time spent vigilant (Mann–Whitney $U_{22,16} = 39$, $p < 0.001$; Fig. 1c). Considering only the proportion of vigilance time spent chewing, animals chewed with the same frequency whatever the type of vigilance (Mann–Whitney $U_{22,16} = 151$, $p = 0.47$; Fig. 1d). In routine vigilance, 21 of 22 individuals did not wait at all before performing the first chew once their neck was raised (Fig. 1e). At the opposite, 16 of 17 animals engaged in induced vigilance delayed their first chew (Fig. 1e), with a mean percentage of time spent without chewing of 37% (range 0%–100%,
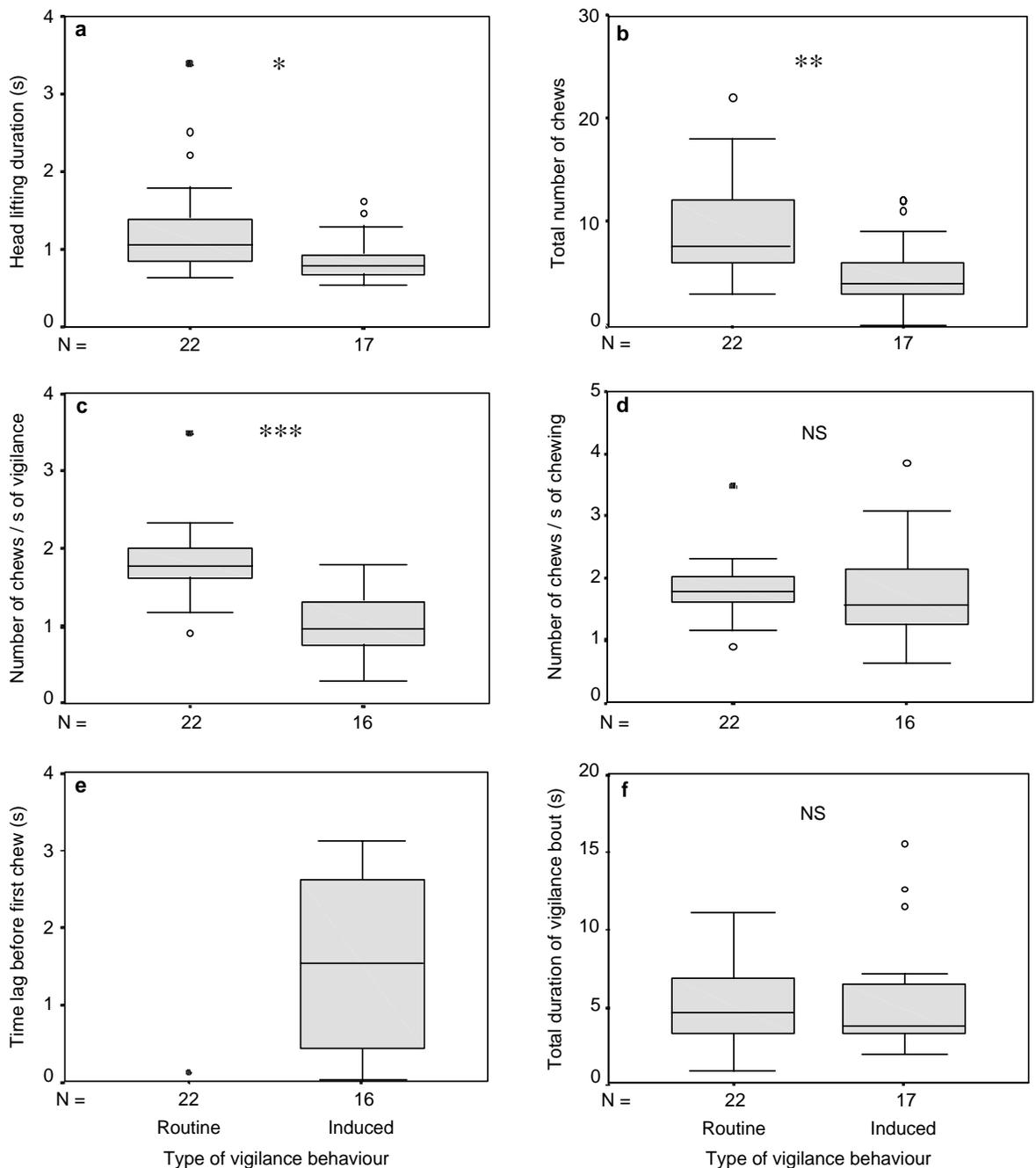
Fig. 1. Head lifting duration (a), total number of chews during a vigilance bout (b), chew frequency while vigilant (c), chew frequency while chewing (d), time lag before first chew (e), and total duration of the vigilance bout (f) according to the type of vigilance behaviour: experimentally induced or routine, in impala observed in Hwange National Park, Zimbabwe. The line across the grey box indicates the median. The box represents the interquartile range containing 50% of values. The whiskers encompass the highest and lowest values, without the open circles, that represent values between 1.5 and 3 box lengths from the upper or lower edge of the box, or filled circles, that are over 3 box lengths. $0.01 <^* <0.05$; $0.001 <^{**} <0.01$; $^{***} <0.001$; NS >0.05.

$CV = 87\%$, if we exclude the one animal that never stopped chewing and another which never chewed the range is 7%–92%). Finally, the duration of vigilance bouts was similar for both groups (Mann–Whitney $U_{22,17} = 175$, $p = 0.75$; Fig. 1f). Group size (range 4–45) was not correlated with any of the recorded

parameters in neither routine (all |Spearman's rho| <0.36; all p values >0.16) nor induced vigilance (all |Spearman's rho| <0.33; all p values >0.21).

Our results suggest that distinguishing between induced and routine vigilance is prudent before investigating the tradeoff between vigilance and foraging. The two vigilance patterns indeed strongly differed. When responding to an external controlled stimulus, impalas raised their head faster, waited for a much longer time before initiating the first chew and chewed less, both in total and by second spent vigilant compared to the situation where the observer did not induce vigilance, i.e. when engaged in routine behaviour. Neither the number of chews per second of chewing nor the total duration time of the bouts depended on the type of vigilance. Therefore, alarmed individuals do not seem to compensate for the discontinuity of the ingestion process by increasing chew frequency or reducing the bout duration. However, the great variability in chewing frequency once resuming chewing during induced vigilance (Fig. 1d) could suggest that some individuals may actually compensate when threat perception is down to an acceptable level whereas individuals still perceiving some risk may on the contrary engage in a low frequency chewing activity to maintain some auditory alertness. The inter individual variability in energetic states or personal histories/temperaments may explain such heterogeneity in behaviour. We cannot rule out the possibility that some individuals considered as being in routine vigilance were in fact responding to a non-identified stimulus. However, given the strong differences we report between the two vigilance patterns, this potential bias is unlikely to have affected our results. Moreover, if present, this bias is expected to decrease the contrast between the two forms of vigilance, hence the differences presented here are at the most minimized.

Since animals considerably reduced chewing when alarmed, probably to listen for predators (and possibly to ensure stabilization of their visual field), the assumption of cost-free vigilance was clearly weak in the case of induced vigilance. Conversely, routine vigilance appeared to fulfil all the assumptions for cost-free scanning in the way predicted by theoretical models (Illius and Fitzgibbon 1994), although to fully demonstrate that routine vigilance was cost-free would require to compare the intake rate of animals when they were scanning and when they were not, while accounting for local variation in food biomass (Fortin et al. 2004a). Hence, induced and routine vigilance should be seen as qualitatively different, whereas empirical vigilance studies generally amalgamate the two or only investigate one. This may be due to the fact that individual vigilance is classically defined in its broadest sense as "a motor act which corresponds to a head lift

interrupting the ongoing activity, and followed by a visual scanning of the environment" (Quenette 1990). Therefore, both induced and routine vigilance could match this definition but related to different ongoing activities: only induced vigilance truly interrupts the ingestion process, while routine vigilance interrupts cropping, the continuity of the ingestion process being allowed by chewing continuously. Consequently, vigilance studies should explicitly incorporate stimuli-induced vigilance bouts (Ruxton and Roberts 1999, Fortin et al. 2004a, Bednekoff and Lima 2005), and even more so when studying foraging as it interrupts a key process, the ingestion. Conversely, routine vigilance is also sometimes overlooked: Yáber and Herrera (1994) "only recorded as alert behaviour (or vigilance behaviour) instances in which the animal was (apparently) intently looking around and not simply when it raised its head to, for instance, chew a mouthful". Similarly, Tchabovsky et al. (2001a) "considered a foraging animal to be vigilant only if it abruptly paused in its activity, including chewing and handling food, and looked either around or intently in one direction".

Several studies aimed to discriminate between different forms of vigilance according to their potential tradeoff with foraging (Arenz and Leger 1999, Lima et al. 1999, Guillemain et al. 2001, Tchabovsky et al. 2001b, Verdolin and Slobodchikoff 2002, Cowlishaw et al. 2004). Here, although based on a small sample size for a single species, our data suggest that two different forms of vigilance occur in ungulates: the ontogeny (presence or absence of a stimulus), the patterns (head movements and chewing investment) and finally the impact on ingestion process (and thus potentially the cost of the scan) strongly differed between induced and routine vigilance (Lima and Bednekoff 1999). Moreover, whereas induced vigilance in our study was probably directed towards a predation threat, routine vigilance might serve multiple purposes, such as scrounging, localization of food patches, monitoring herd spatial distribution and identifying escape routes, among others.

A metric of the relative proportion between induced and routine vigilance in a foraging sequence is the next step to further explore these hypotheses. Although the level of routine vigilance should be strongly determined by factors influencing the amount of spare time available while foraging (such as food characteristics) and induced vigilance should be closely tied to external stimuli, animals still have flexibility to adjust both types of vigilance to the individual perception of risk. Foragers may increase the number of routine vigilance bouts by chewing smaller mouthfuls during head-ups. This increase has possible costs due to the loss of chewing efficiency and greater energy expenditure. In the case of induced vigilance, individuals could broaden the range of possible stimuli that trigger the vigilance

bout, as well as decrease the intensity threshold of a given stimulus before they react, thereby increasing the likelihood of interruption in foraging. Contrary to routine vigilance, induced vigilance levels should be largely independent of food characteristics.

As animals may adjust either type of vigilance, the impact on ingestion process may be context-specific. We predict that adjustment in routine vigilance should be related both to changes in environmental variables associated with predation risk (i.e. indirect cues, such as visibility, distance to cover or time of the day, Thorson et al. 1998) and to changes in the prey's information about the predator's presence (following Brown et al. 1999, a prey may or may not be aware of the presence/absence of a predator or may have imperfect information). For instance, a prey with no information about a predator's potential presence, feeding far away from a refuge (such as a cliff), may engage in routine vigilance with the same frequency as a prey feeding closer to a refuge and aware of the presence of a predator. Adjustment in the likelihood to engage in induced vigilance may occur in two ways. First, it could parallel adjustments in routine vigilance level, since both types of vigilance are related to individual perception of risk. Because induced vigilance is more costly, however, animals experiencing an increase in risk should first increase routine vigilance level, while those experiencing a decrease in risk should first decrease the likelihood to engage in induced vigilance. Second, as the intensity and/or number of direct cues of predation risk (e.g. visual or auditory stimuli) increases, information about the predator becomes more accurate (which predator, where, how many of them . . .). Under such circumstances, prey may focus their attention on stimuli specific to the particular situation, and thus decrease the intensity threshold for them to trigger induced vigilance.

In the context of the ecology of fear (sensu Brown et al. 1999), distinguishing between the two types of vigilance may help to identify the mechanisms and associated costs related to how animals adjust vigilance behaviour as they update their assessment of predation risk. Future field studies should also investigate how the factors usually reported to affect vigilance behaviour, such as group size, habitat characteristics or position within the herd, among many others (Quenette 1990), impact on the routine and induced vigilance responses, and further, on time being vigilant without chewing.

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