

# Influence of Different Individual Traits on Vigilance Behaviour in European Rabbits

Raquel Monclús\*,† & Heiko G. Rödel†

\* Unidad de Zoología, Dpto. Biología, Universidad Autónoma de Madrid, Madrid, Spain

† Department of Animal Physiology, University of Bayreuth, Bayreuth, Germany

## Correspondence

Raquel Monclús, Unidad de Zoología, Dpto. Biología, Universidad Autónoma de Madrid, 28049 Madrid, Spain.

E-mail: raquel.monclus@uam.es

Heiko G. Rödel, Department of Animal Physiology, University of Bayreuth, D-95440 Bayreuth, Germany.

E-mail: heiko.roedel@uni-bayreuth.de

Received: February 3, 2009

Initial acceptance: March 2, 2009

Final acceptance: April 21, 2009

(K. Reinhold)

doi: 10.1111/j.1439-0310.2009.01661.x

## Abstract

An animal's level of vigilance depends on various environmental factors such as predator presence or the proximity of conspecific competitors. In addition, several individual traits may influence vigilance. We investigated the effects of body condition, social rank and the state of pregnancy on individual vigilance (scanning) rates in individually marked European rabbits (*Oryctolagus cuniculus*) of a field enclosure population. We found lower rates in young rabbits than in adult females, but male and female juveniles did not differ. Vigilance of juveniles was positively correlated with their age-dependent body mass (used as a measure of body condition), i.e. young rabbits with lower body condition scanned less. We suggest that juveniles with low body condition were trading off vigilance against feeding to maximise their growth. In contrast, there was no significant correlation between body mass and vigilance in adult females. Adult females increased scanning rates during late pregnancy, which might constitute a behavioural compensation because of their lower capacity to escape predator attacks. In addition, adult females with low social ranks scanned more than high ranking individuals, likely because of their higher risk of attacks by conspecifics. In summary, our results highlight various individual characteristics that influence vigilance behaviour in European rabbits.

## Introduction

Vigilance is a common anti-predator strategy in mammals and birds (Elgar 1989; McDonough & Loughry 1995; Robinette & Ha 2001; Monclús et al. 2005, 2006). Scanning animals are able to detect and may deter the attacks of potential predators. Thus, the survival of an animal might be related to individual vigilance rates (FitzGibbon 1989; Scannell et al. 2001). Above all, the level of anti-predator vigilance depends on the perceived predation risk, which in turn depends on environmental cues (Moreno et al. 1996; Kotler et al. 2002), group size (Roberts 1996; Di Blanco & Hirsch 2006), or social factors (Cameron & du Toit 2005; Lung & Childress

2007; Monclús & Rödel 2008). However, under similar ecological conditions, animals often react differently to predation risk, and individual traits may lead to differences in the perception of the risk and consequently to differences in anti-predator vigilance (DeWitt et al. 1999).

Some studies report correlations of vigilance (scanning) rates with parameters such as an animal's size, body condition or previous experience with predators. Age might also play an important role. Young animals usually undergo higher predation pressure than adults (Chase 1999). Moreover, very young animals tend to respond to any novel stimulus given that the costs associated with failing to recognise a predator are higher than the costs associated with

responding to innocuous stimuli, i.e. the behavioural responses in early life are often generalised and become more specific with age and experience (quantitative response hypothesis; Inglis 1979). This might result in juveniles showing higher vigilance rates than adults (Mateo 1996; Hanson & Coss 2001; Avilés & Bednekoff 2007). On the other hand, some studies have reported lower vigilance rates in juveniles (Arenz & Leger 2000; Hanson & Coss 2001; Lohrer et al. 2005) probably because of age-specific differences in the animals' basic requirements: Juveniles have high nutritional and feeding requirements and feeding can compete with anti-predator behaviours in animals of this age class.

Apart from age, other individual factors such as sex, social rank and body condition might affect vigilance rates (Elgar 1989). Variation in these traits, which are usually related to vulnerability or energetic reserves, may explain the huge differences among individuals within an age class (DeWitt et al. 1999). For instance, body condition (often measured by age-specific body mass) is a critical factor for winter survival of young animals (Marboutin & Hansen 1998; Rödel et al. 2004). Given that high vigilance rates can be costly for an animal, individuals in poor body condition might trade off vigilance against growth or feeding (Preisser et al. 2005). On the other hand, animals might increase their vigilance rates when their risk of predation is unusually high. This might apply to pregnant females, or more generally to females during the breeding season, which are frequently reported to have an increased risk of predation mortality (Klemola et al. 1997; Norrdahl & Korpimäki 1998; Kraus & Rödel 2004). Pregnant females are physically restricted in their abilities to escape a predator attack, especially during late pregnancy, when the animals usually show an increase in body mass, reducing their agility. The consequences on the vigilance rates of pregnant females might be particularly pronounced in subordinate individuals, which do not only have to scan for predators but may also have to monitor other group members to avoid aggressive encounters (Monclús & Rödel 2008).

We studied the relationships between different individual characteristics and vigilance rates in European rabbits (*Oryctolagus cuniculus* L.). This was carried out with animals from an individually marked population living in a field enclosure. We observed adult females and juveniles of both sexes during summer (mid-breeding season) and autumn (non-breeding season). Based on the assumption that juveniles with a low body condition might trade off

growth (i.e. feeding) against vigilance, we (i) predicted a positive correlation between their age-specific body mass and vigilance rates. We also tested this expectation in adult females by looking at the correlations between body mass and vigilance during and after the breeding season. We (ii) compared vigilance rates between low ranking and high ranking adult females. We expected low ranking females to show higher rates to avoid attacks from higher ranking females. We (iii) tested for differences in vigilance during different stages of pregnancy and expected vigilance rates to be highest during late pregnancy, when the agility of the females is low.

## Methods

### Study Population and Study Period

We conducted our study on animals from an individually marked population of European rabbits living in a field enclosure of 2 ha on the campus of the University of Bayreuth, Upper Franconia, Germany. The animals were descendants of individuals that had been caught in the wild in 1983. The enclosure consisted of grassland interspersed with groups of trees and bushes. The animals lived in an undisturbed semi-natural environment. During the period of behavioural observations (2004, 2006), the adult population density varied between 42 and 52 animals.

In addition to the burrows and breeding stops (i.e. short breeding burrows) dug by the rabbits (around 40), the area contained 16 artificial concrete warrens with interconnecting chambers and removable tops. These were used by the rabbits as main warrens of their group territories and also for breeding.

We restricted the access of terrestrial predators (e.g. *Martes foina*, *Mustela erminea*) by a double electric wire (cattle fence), installed along the outer side of the enclosure fence at a height of 3 and 1.5 m. However, birds of prey (in particular common buzzards *Buteo buteo*) still preyed heavily on juveniles during the first few weeks after their emergence above ground.

European rabbits living in the temperate zones usually start to reproduce during the breeding season after their year of birth, when they are around 1-yr old. Therefore, the animals were referred to as 'juveniles' until they had survived the winter.

The entire study site could be observed from two outlook towers and all animals could be identified by their individual ear-tags. For further details on the study population see von Holst et al. (2002).

## Study Animals

Every morning during the breeding season, we checked for newborn litters. For this, we prepared all warrens and breeding stops dug by the animals with artificial vertical openings to the nest chambers, which we covered with concrete flagstones. We knew the date of birth of every juvenile, which we observed during summer or autumn. At postnatal day 12, we determined the sex of the pups and marked them individually with numbered plastic tags (Dalton Rototag,  $20 \times 5 \times 1$  mm, 0.25 g). Prior to the start of the behavioural observations, we replaced the small plastic tags with coloured aluminium tags ( $45 \times 20$  mm, 1.1 g), which are easier to identify from the observation towers with binoculars.

We trapped the adult females during the breeding season (see details in Rödel et al. 2008) and individually dyed their abdominal fur with different colours (silk colour; Marabu, Germany). As female rabbits pluck out their abdominal fur to build their nests (Denenberg et al. 1963), we were able to determine the mother of each litter by the location of the nest in combination with the colour of the fur found in it. Identity of the mothers was additionally confirmed by the analysis of females' reproductive status during the regular trapping sessions (detection of pregnancies by abdominal palpation) and by behavioural observations (females entering particular breeding burrows; copulation as a sign of postpartum oestrus; nest defence against other females, Rödel et al. 2008). Females in late pregnancy were immediately released, and we are not aware of any cases of pregnant females losing their litters following trapping.

## Behavioural Observations

### *Vigilance*

We measured vigilance by focal animal sampling, where we continuously recorded the occurrence of scanning events while the animals were feeding using binoculars (Martin & Bateson 1993). Observations were performed during 3–5 d/wk. Focal animals were observed continuously for 30 min/d during the last 3–4 h before twilight from one of the two towers. During this time, European rabbits show their main daily activity (Wallage-Drees 1989). We considered the animals to be vigilant when they showed signs of alertness, such as lifting the ears, raising the head or looking around, independently whether they stopped their normal activity or not (Monclús et al. 2005; Rödel et al. 2006).

We observed 20 juvenile rabbits for 2 mo during summer (early Jul. to late Aug.) in 2006 and another 17 juveniles for 2 mo during autumn (mid Oct. to mid Dec.) in 2004. Furthermore, we observed 12 different adult females during the breeding season 2006 from early May until mid Sept., and 15 adult females during the non-breeding season from mid Oct. to mid Dec. 2004. On average, each animal was observed for 4–6 h/mo. Adult males were not observed because of their low numbers at the study site. We did not consider the feeding group size of our focal animals, although it is considered to have an effect on individual vigilance in some species (Pulliam 1973; Roberts 1996; Fairbanks & Dobson 2007; but see Robinette & Ha 2001; Cameron & du Toit 2005). In a previous study, we showed that feeding group size (i.e. the number of animals feeding in close proximity) does not affect individual scanning rates of European rabbits (Monclús & Rödel 2008), probably because feeding groups are usually rather small (2.5 individuals on average) and the composition of individuals per group fluctuates strongly.

### *Social rank and group membership*

During behavioural observations, we ascertained group membership and the social ranks of all adult females. The social system of the rabbit is characterised by sex-specific linear rank hierarchies (Mykytowycz 1959; von Holst et al. 2002). We determined the social rank of each adult female by the occurrence and direction of aggression (within the social group) among females, such as chases and displacements (see von Holst et al. 2002). During the study period, the number of females per social group varied between 2 and 7.

## Individual Traits

### *Body mass*

We determined the body masses of the animals during the monthly trapping sessions. The animals were caught using 100 peanut-baited wooden live traps, which were evenly distributed in the study area. Trapped animals were kept separately in gunny sacks, were weighed and then released in the study area.

The body mass for each female during the breeding season was calculated by averaging the body masses of the respective female obtained during the monthly trapping sessions from Mar. to Jun. 2006, i.e. shortly before we recorded vigilance behaviour

during gestation. For each female we obtained at least three measurements of body mass. This was performed to minimise biases caused by the state of pregnancy when the females were weighed. During the non-breeding season (2004), we measured female body masses in mid Nov.

#### *Age-specific body mass of juveniles*

Since the body mass of juvenile rabbits is mainly a function of their age, we used the age-specific body mass (corrected for age) as a measure of body condition in animals of this age class (Rödel et al. 2004). For this, we fitted Gompertz functions to the relationship between age and body mass of juveniles caught in mid Aug. ( $n = 185$ ; Fig. 1a) and mid Nov. ( $n = 288$ ; Fig. 1b) (Zullinger et al. 1984). These data were collected over six different years (1998–2001; 2004; 2006). We then calculated the unstandardised residuals (i.e. the difference between the measured and the predicted body mass) for each of our focal animals, based on their body masses measured in Aug. (for the juveniles observed in summer) and in Nov. (for the juveniles observed in autumn). Positive or negative residuals imply that the animals were heavier or lighter than predicted by the model fit, respectively. The regression models were highly significant for juveniles of both age classes (Fig. 1a, b).

#### *Reproductive status of adult females*

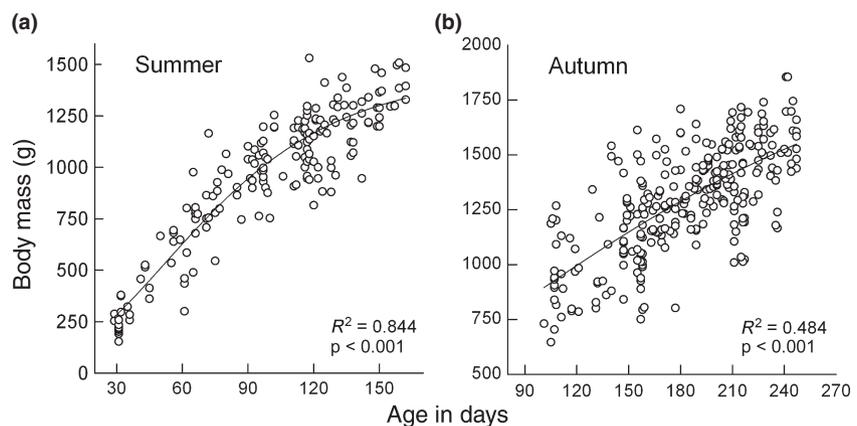
The females' stage of gestation was assessed retrospectively. Since we knew the mother of every litter and the date of parturition, we could calculate the mother's day of conception by subtracting 30 d from the date of parturition (Brambell 1944). We then divided the females' gestation period into three parts:

early (from conception to day 10), mid (from day 11 to 20) and late gestation (from day 21 to 30).

#### **Sample Size and Data Analysis**

The goal of the study was to test the effects of different individual characteristics on an animal's frequency of vigilance. This was performed using multivariate linear models (LM) or linear-mixed models (LMM), calculated with the software package R version 2.8.0 (R Development Core Team 2008). LMM were calculated with the package lme4 (Bates 2005) using maximum likelihood estimators. p-Values were extracted using likelihood ratio tests based on the changes when each term was dropped from the full (main effects) model. Interactions were tested by considering the changes when these were added to the model (Faraway 2006). When using LM, we removed non-significant covariate interaction terms and present the p-values of the main effects model (Engqvist 2005). We ensured that the residuals of all models approximated to a normal distribution by visually checking normal probability plots and by the Shapiro–Wilk test. Vigilance behaviour of some data sets showed a slightly right-skewed distribution and was then  $[x^{0.2}]$  transformed prior to analysis to adjust the data to a normal distribution.

In total, we analysed four different data sets from 2 yr. We tested the effects of body condition (i.e. age-specific body mass), age and sex on vigilance rates of juvenile rabbits observed during summer 2006 ( $n = 20$  from 11 different litters; 11 males and nine females) and during autumn 2004 ( $n = 17$  from 17 different litters; seven males and 10 females). Some of the juveniles observed in summer were litter mates and therefore experienced similar early life conditions, which might have influenced their



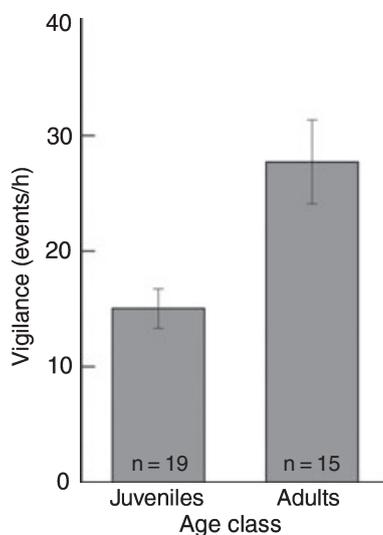
**Fig. 1:** Relationship between age and body mass of juvenile European rabbits in (a) summer and in (b) autumn. Regression lines are fitted by a Gompertz function [ $y = a \times \exp(-\exp(-(x - x_0)/b))$ ]; Zullinger et al. 1984). Data stem from  $n = 185$  juveniles trapped in mid Aug. and from  $n = 288$  juveniles trapped in mid Nov. during six different years, see graphs for statistics. Note the differences in the scaling of the y-axis.

vigilance behaviour in a similar way. To account for such potential litter effects, we included litter identity as a random factor. We also analysed data collected from adult females. Our data set during the mid/late breeding season in 2006 (May–Sept.) was based on behavioural observations of 12 different females; each female reproduced among one and three times resulting in a total of 25 gestations. During the non-breeding season (Oct.–Dec. 2004), we observed another 15 females. During the breeding season, we compared the vigilance behaviour among females in early, mid and late stages of pregnancy. In addition, we tested the effects of social rank (fixed factor with two levels: high ranking: rank 1 and 2; low ranking: >rank 2) and body mass. For the analysis, we used LMM, where we included female identity as a random factor to account for the (unbalanced) repeated observations of the same females during successive gestations (up to three per female).

## Results

### Comparison of Juveniles and Adults

Vigilance rates in adult females were significantly higher than in juveniles (both sexes) (independent samples t-test:  $t_{30} = -3.43$ ,  $p = 0.001$ ). On average, adult females showed about 90% higher vigilance rates than juveniles (Fig. 2). Such significant differences were found in comparison with male ( $t_{20} = -2.57$ ,  $p = 0.018$ ) as well as to female juveniles ( $t_{23} = -2.97$ ,  $p = 0.007$ ).



**Fig. 2:** Vigilance (scanning) rates (means  $\pm$  SE) in juvenile (males and females) and adult female European rabbits. See text for statistics.

In mid Nov. 2004, when these behavioural observations were carried out, adult animals had significantly higher body masses than our focal juveniles, which were all born between late May and late Jul. of that breeding season (juvenile females vs. adult females:  $t_{26} = -8.74$ ,  $p < 0.001$ ; juvenile males vs. adult males:  $t_{14} = -8.39$ ,  $p < 0.001$ ). Juvenile females ( $n = 10$ ) weighed 1121 g ( $\pm 76$  SE) and juvenile males ( $n = 7$ ) weighed 1216 g ( $\pm 62$  SE). The average body mass of adults was 1704 g ( $\pm 18$  SE) in males ( $n = 9$ ), and 1691 g ( $\pm 25$  SE) for females ( $n = 18$ ).

### Traits Affecting Vigilance in Juveniles

We found positive correlations between the juveniles' age-specific (residual) body mass and the vigilance rate observed in juveniles during the summer (LMM:  $\chi^2 = 7.00$ ,  $p = 0.008$ ; Fig. 3a) as well as in individuals observed in autumn (LM:  $F_{1,13} = 7.20$ ,  $p = 0.018$ ; Fig. 3b). In both seasons, the juveniles' vigilance rate did not differ between males and females (summer:  $\chi^2 = 0.24$ ,  $p = 0.63$ ; autumn:  $F_{1,13} = 0.28$ ,  $p = 0.61$ ). The interactions between the age-specific body mass and sex were also not statistically significant ( $p > 0.10$ ) and were removed from the final models.

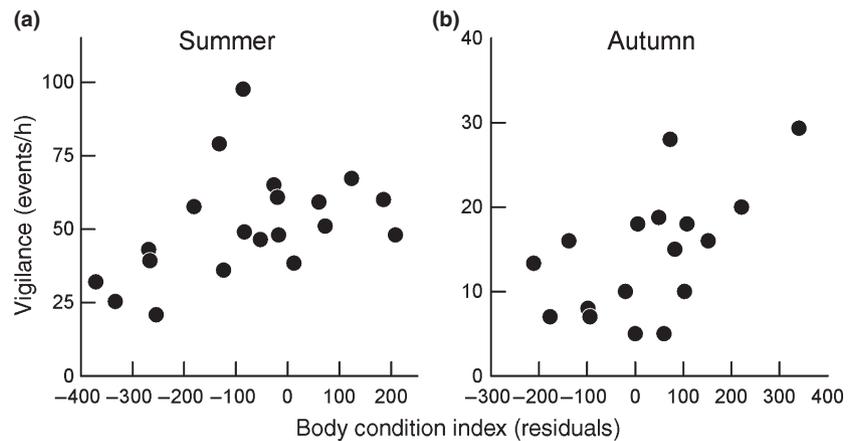
### Traits Affecting Vigilance in Adult Females

#### Breeding season

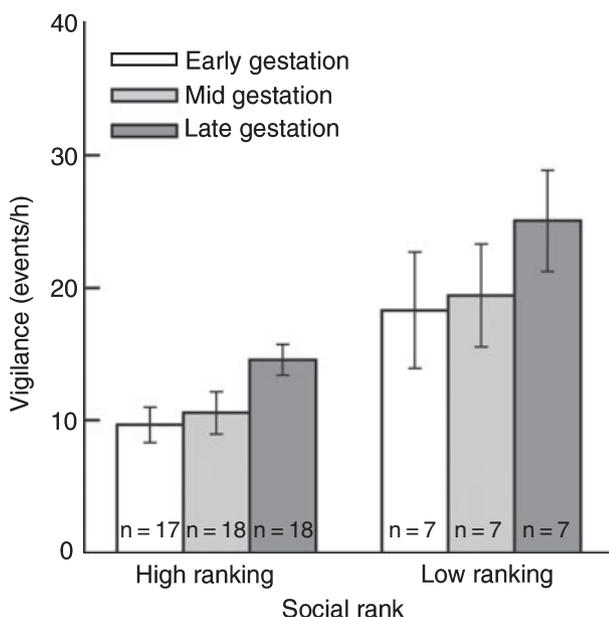
During the breeding season, the females' gestational state significantly affected their vigilance behaviour (LMM:  $\chi^2 = 20.72$ ,  $p < 0.001$ ; Fig. 4). Females were significantly more vigilant during late pregnancy than during mid (*post hoc*: paired t-test:  $t_{23} = -3.23$ ,  $p = 0.004$ ) and early gestation ( $t_{23} = -3.69$ ,  $p = 0.001$ ), whereas vigilance levels during early and mid gestation did not differ ( $t_{23} = -1.11$ ,  $p = 0.28$ ). Furthermore, females with high social rank positions (rank 1 and 2) showed significantly lower vigilance rates than low ranking individuals ( $\chi^2 = 4.31$ ,  $p = 0.038$ ; Fig. 4). Female body mass did not affect the rate of vigilance ( $\chi^2 = 0.08$ ,  $p = 0.78$ ). None of the two-way interactions between the tested independent variables was statistically significant ( $p > 0.10$ ).

#### Non-breeding season

In autumn, shortly after the breeding season, we did not find any significant effects of the females' social rank (LM:  $F_{1,12} = 0.15$ ,  $p = 0.71$ ), or body mass



**Fig. 3:** Correlation between the vigilance (scanning) rates of juvenile European rabbits in (a) summer and (b) autumn and their age-specific body mass (see Fig. 1 for calculation). Note the differences in the scaling of the x- and y-axes; see text for statistics.



**Fig. 4:** Vigilance (scanning) rates (means  $\pm$  SE) of high-ranking (social rank 1 + 2) and low ranking (>rank 2) European rabbit females during early, mid and late gestation. See text for statistics.

( $F_{1,12} = 0.01$ ,  $p = 0.95$ ) on vigilance rates. The interaction of the two explanatory variables was also not significant ( $p > 0.10$ ).

**Discussion**

Vigilance rates were about 90% higher in adult females than in juveniles. In accordance with our predictions, vigilance in juveniles was positively correlated with their age-specific body mass. Vigilance was not related to body mass in adult females either during or after the breeding season. However, we found an increase of vigilance in adult females from early to late pregnancy, and higher

vigilance levels in low-ranking than in high-ranking females.

Young post-weaned European rabbits showed comparatively lower vigilance rates than adults, even though they usually experience comparatively higher predation rates (Parer 1977; Chase 1999). Such lower vigilance in juveniles has also been found in other studies of mammals (Arenz & Leger 2000; Hollén et al. 2008) and several hypotheses have been suggested to explain this finding: First, experience may play an important role and juveniles might still need to hone their skills in detecting predators (Griffin et al. 2000; Kavaliers et al. 2003). Second, younger animals might show lower vigilance rates as the display of this behaviour competes with energy gain, and juveniles might be more energetically constrained than adults (FitzGibbon 1989; DeWitt et al. 1999; Arenz & Leger 2000; Murray 2002; Winnie & Creel 2007). Both empirical and theoretical studies have highlighted that animals frequently compensate for food stress by accepting a higher predation risk, rather than vice versa (Bachman 1993; Oksanen & Lundberg 1995; Stone 2007). In particular, our findings are in accordance with the second, the energy constrain hypothesis, as interestingly our results suggest that this trade-off between energy gain and vigilance is not only apparent between but also within an age class: In juveniles, vigilance rates were positively related to their body condition, i.e. young rabbits with a lower age-specific body mass were less vigilant. This positive correlation was apparent in two sets of juveniles observed during two different years. Young mammals might have conflicting demands between growth and defence (resource allocation trade-off: Steiner & Pfeiffer 2007), especially in temperate climates where winter mortality is high and survival to the next season strongly depends on the body mass

attained at the end of the vegetation period (Marboutin & Hansen 1998; European rabbits: Rödel et al. 2004). Therefore, juveniles in poor body condition should make a greater effort to fulfil their energetic requirements. However, we did not find such a relationship in adult females; there was no correlation between female body mass and vigilance rate, even during the energetically demanding reproductive season (but see Murray 2002; Winnie & Creel 2007 for examples of such trade-offs in adult animals).

Vigilance rates of juveniles in summer were much lower than in autumn (Fig. 3a, b). However, both data sets were collected during different years, and we do not know whether these differences would occur between seasons on an individual basis, or if they are just the consequence of unidentified environmental differences between years.

Pregnant females showed a significant increase in vigilance as pregnancy progressed. As a result of mass gain, especially during the last stages of gestation, female rabbits might be restricted in their ability to run to the shelter of their burrows, leading to a higher risk of predation (Klemola et al. 1997). They might therefore compensate for their reduced ability by increasingly scanning for potential predators. Such behavioural compensation for reduced locomotor ability has also been found in other species. For example, gravid collared lizards (*Crotaphytus collaris*) stay closer to their refuges and therefore shorten the distance they run when escaping (Husak 2006), and gravid keelbacks (*Tropidonophis mairii*) increase the flight distance in response to predators (Brown & Shine 2004). In addition, an increase in intrasexual competition might have also contributed to the observed increase in scanning rates during the last stage of pregnancy, because a female might increasingly direct vigilance to other pregnant females which may attempt to take over her breeding burrow (Rödel et al. 2008).

Vigilance rates of pregnant females also depended on their social rank, with low ranking females scanning more than high ranking ones. Generally, vigilance in European rabbits (and most probably also in other social mammals) serves at least two functions: the detection of predators and conspecific competitors (Monclús & Rödel 2008). During the breeding season, females compete for the access to favourable breeding sites or burrows, sometimes by highly aggressive encounters (Myers & Poole 1961; von Holst et al. 1999; Rödel et al. 2008). During this season, subordinate females are chased or displaced by the more dominant ones. Higher vigilance rates may

allow them to avoid such agonistic encounters. In addition, vigilance may also serve to prevent infanticide (Steenbeek et al. 1999; but see Manno 2007), and probably nests of subordinate mothers are more prone to infanticidal episodes, leading to higher vigilance in low ranking females. Such killing of dependent young by conspecifics has been described for European rabbits, and other adult females are proposed to be the perpetrators (Künkele 1992; Rödel et al. 2008).

The results of our observational study suggest how life-history traits relate to different ontogenetic stages, and therefore, to different requirements influencing vigilance rates in European rabbits. However, how and to what extent such individual differences in vigilance affect predation mortality and the fitness of an animal is not known and could be an interesting topic for further studies.

### Acknowledgements

Thanks to A. Deibl, C. Kurz, A. Starkloff and F. Weber, who kindly helped with the data collection. We are indebted to D. von Holst for his support and valuable comments and to R. Hudson for correcting the English. We are also grateful to K. Reinhold and two anonymous reviewers for their constructive comments on early drafts of the manuscript. Thanks to F. Locke for social support. Permission for population biology studies on European rabbits was granted by the government of Middle Franconia (211–3894a).

### Literature Cited

- Arenz, C. L. & Leger, D. W. 2000: Antipredator vigilance of juvenile and adult thirteen-lined ground squirrels and the role of nutritional need. *Anim. Behav.* **59**, 535–541.
- Avilés, J. M. & Bednekoff, P. A. 2007: How do vigilance and feeding by common cranes *Grus grus* depend on age, habitat, and flock size? *J. Avian Biol.* **38**, 690–697.
- Bachman, G. C. 1993: The effect of body condition on the trade-off between vigilance and foraging in Belding's ground squirrels. *Anim. Behav.* **46**, 233–244.
- Bates, D. 2005: Fitting linear mixed models in R. *R. News* **5**, 27–39.
- Brambell, F. W. R. 1944: The reproduction of the wild rabbit *Oryctolagus cuniculus* (L.). *Proc. Zool. Soc. Lond.* **114**, 1–45.
- Brown, G. P. & Shine, R. 2004: Effects of reproduction on the antipredator tactics of snakes (*Tropidonophis*

- mairii*, Colubridae). *Behav. Ecol. Sociobiol.* **56**, 257–262.
- Cameron, E. Z. & du Toit, J. T. 2005: Social influences on vigilance behaviour in giraffes, *Giraffa camelopardalis*. *Anim. Behav.* **69**, 1337–1344.
- Chase, J. M. 1999: To grow or to reproduce? The role of life-history plasticity in food web dynamics. *Am. Nat.* **154**, 571–586.
- Denenberg, V. H., Huff, R. L., Ross, S., Sawin, P. B. & Zarrow, M. X. 1963: Maternal behaviour in the rabbit: the quantification of nest building. *Anim. Behav.* **11**, 494–499.
- DeWitt, T. J., Sih, A. & Hucko, J. A. 1999: Trait compensation and cospecialization in a freshwater snail: size, shape and antipredator behaviour. *Anim. Behav.* **58**, 397–407.
- Di Blanco, Y. & Hirsch, B. T. 2006: Determinants of vigilance behavior in the ring-tailed coati (*Nasua nasua*): the importance of within-group spatial position. *Behav. Ecol. Sociobiol.* **61**, 173–182.
- Elgar, M. A. 1989: Predator vigilance and group size in mammals and birds: a critical review of the empirical vigilance. *Biol. Rev.* **64**, 13–33.
- Engqvist, L. 2005: The mistreatment of covariate interaction terms in linear model analyses of behavioural and evolutionary ecology studies. *Anim. Behav.* **70**, 967–971.
- Fairbanks, B. & Dobson, S. 2007: Mechanisms of the group-size effect on vigilance in Columbian ground squirrels: dilution versus detection. *Anim. Behav.* **73**, 115–123.
- Faraway, J. 2006: *Extending the Linear Model with R*. Chapman & Hall/CRC, New York.
- 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.
- Griffin, A. S., Blumstein, D. T. & Evans, C. S. 2000: Training captive-bred or translocated animals to avoid predators. *Conserv. Biol.* **14**, 1317–1326.
- Hanson, M. T. & Coss, R. G. 2001: Age differences in arousal and vigilance in California ground squirrels (*Spermophilus beecheyi*). *Dev. Psychobiol.* **39**, 199–206.
- Hollén, L. I., Clutton-Brock, T. H. & Manser, M. 2008: Ontogenetic changes in alarm-call production and usage in meerkats (*Suricata suricatta*): adaptations or constraints? *Behav. Ecol. Sociobiol.* **62**, 821–829.
- von Holst, D., Hutzelmeyer, H., Kaetzke, P., Khaschei, M. & Schonheiter, R. 1999: Social rank, stress, fitness, and life expectancy in wild rabbits. *Naturwissenschaften* **86**, 388–393.
- von Holst, D., Hutzelmeyer, H. D., Kaetzke, P., Khaschei, M., Rödel, H. G. & Schrutka, H. 2002: Social rank, fecundity and lifetime reproductive success in wild European rabbits (*Oryctolagus cuniculus*). *Behav. Ecol. Sociobiol.* **51**, 245–254.
- Husak, J. F. 2006: Do female collared lizards change field use of maximal sprint speed capacity when gravid? *Oecologia* **150**, 339–343.
- Inglis, I. R. 1979: Visual bird scarers: an ethological approach. In: *Bird Problems in Agriculture* (Wright, E. N., Inglis, I. R. & Feare, C. J., eds). MAFF Publishers, London, pp. 121–143.
- Kavaliers, M., Colwell, D. D. & Choleris, E. 2003: Learning to fear and cope with a natural stressor: individually and socially acquired corticosterone and avoidance responses to biting flies. *Horm. Behav.* **43**, 99–107.
- Klemola, T., Koivula, M., Korpimäki, E. & Norrdahl, K. 1997: Small mustelid predation slows population growth of *Microtus* voles: a predator reduction experiment. *J. Anim. Ecol.* **66**, 607–614.
- Kotler, B. P., Brown, J. S., Dall, S. R. X., Gresser, S., Ganey, D. & Bouskila, A. 2002: Foraging games between gerbils and their predators: temporal dynamics of resource depletion and apprehension in gerbils. *Evol. Ecol. Res.* **4**, 495–518.
- Kraus, C. & Rödel, H. G. 2004: Where have all the cavies gone? Causes and consequences of predation by the minor grison for a wild cavy population. *Oikos* **105**, 489–500.
- Künkele, J. 1992: Infanticide in the wild rabbit (*Oryctolagus cuniculus*). *J. Mammal.* **73**, 317–320.
- Loehr, J., Kovanen, M., Carey, J., Hogmänder, H., Jurasz, C., Karkkainen, S., Suhonen, J. & Ylönen, H. 2005: Gender- and age-class-specific reactions to human disturbance in a sexually dimorphic ungulate. *Can. J. Zool.* **83**, 1602–1607.
- Lung, M. A. & Childress, M. J. 2007: The influence of conspecifics and predation risk on the vigilance of elk (*Cervus elaphus*) in Yellowstone National Park. *Behav. Ecol.* **18**, 12–20.
- Manno, T. G. 2007: Why are Utah prairie dogs vigilant? *J. Mammal.* **88**, 555–563.
- Marboutin, E. & Hansen, K. 1998: Survival rates in a nonharvested brown hare population. *J. Wildl. Manage.* **62**, 772–779.
- Martin, P. & Bateson, P. 1993: *Measuring Behaviour. An Introductory Guide*. Cambridge Univ. Press, Cambridge.
- Mateo, J. M. 1996: The development of alarm-call response behaviour in free-living juvenile Belding's ground squirrels. *Anim. Behav.* **52**, 489–505.
- McDonough, C. M. & Loughry, W. J. 1995: Influences on vigilance in nine-banded armadillos. *Ethology* **100**, 50–60.
- Monclús, R. & Rödel, H. G. 2008: Different forms of vigilance in response to the presence of predators and conspecifics in a group-living mammal, the European rabbit. *Ethology* **114**, 287–297.
- Monclús, R., Rödel, H. G., von Holst, D. & de Miguel, J. 2005: Behavioural and physiological responses of naive

- European rabbits to predator odour. *Anim. Behav.* **70**, 753–761.
- Monclús, R., Rödel, H. G. & von Holst, D. 2006: Fox odour increases vigilance in European rabbits: a study under semi-natural conditions. *Ethology* **112**, 1186–1193.
- Moreno, S., Villafuerte, R. & Delibes, M. 1996: Cover is safe during the day but dangerous at night: the use of vegetation by European wild rabbits. *Can. J. Zool.* **74**, 1656–1660.
- Murray, D. L. 2002: Differential body condition and vulnerability to predation in snowshoe hares. *J. Anim. Ecol.* **71**, 614–625.
- Myers, K. & Poole, W. E. 1961: A study of the biology of the wild rabbit, *Oryctolagus cuniculus* (L.), in confined populations. II. The effects of season and population increase on behaviour. *CSIRO Wildl. Res.* **6**, 1–41.
- Mykutowycz, R. 1959: Social behaviour of an experimental colony of wild rabbits, *Oryctolagus cuniculus* (L.). II. First breeding season. *CSIRO Wildl. Res.* **4**, 1–13.
- Norrdahl, K. & Korpimäki, E. 1998: Does mobility or sex of voles affect risk of predation by mammalian predators. *Ecology* **79**, 226–232.
- Oksanen, L. & Lundberg, P. 1995: Optimization of reproductive effort and foraging time in mammals: the influence of resource level and predation risk. *Evol. Ecol.* **9**, 45–56.
- Parer, I. 1977: The population ecology of the wild rabbit, *Oryctolagus cuniculus* (L.) in a Mediterranean type climate in New South Wales. *Aust. Wildl. Res.* **4**, 171–205.
- Preisser, E. L., Bolnick, D. I. & Benard, M. F. 2005: Scared to death? The effects of intimidation and consumption in predator-prey interactions *Ecology* **86**, 501–509.
- Pulliam, H. R. 1973: On the advantages of flocking. *J. Theor. Biol.* **38**, 419–422.
- R Development Core Team 2008: R: A Language and Environment for Statistical Computing. R Foundation for Statistical Computing, Vienna. ISBN: 3-900051-07-0. Available at: <http://www.R-project.org> (last accessed 1 October 2008).
- Roberts, G. 1996: Why individual vigilance declines as group size increases. *Anim. Behav.* **51**, 1077–1086.
- Robinette, R. L. & Ha, J. C. 2001: Social and ecological factors influencing vigilance by northwestern crows, *Corvus caurinus*. *Anim. Behav.* **62**, 447–452.
- Rödel, H. G., Bora, A., Kaetzke, P., Khaschei, M., Hutzelmeyer, H. & von Holst, D. 2004: Over-winter survival in subadult European rabbits: weather effects, density dependence, and the impact of individual characteristics. *Oecologia* **140**, 566–576.
- Rödel, H. G., Monclús, R. & von Holst, D. 2006: Behavioral styles in European rabbits: social interactions and responses to experimental stressors. *Physiol. Behav.* **89**, 180–188.
- Rödel, H. G., Starkloff, A., Bautista, A., Friedrich, A. C. & von Holst, D. 2008: Infanticide and maternal offspring defence in European rabbits under natural breeding conditions. *Ethology* **114**, 22–31.
- Scannell, J., Roberts, G. & Lazarus, J. 2001: Prey scan at random to evade observant predators. *Proc. R. Soc. B* **268**, 541–547.
- Steenbeek, R., Piek, R. C., van Buul, M. & van Hooff, J. A. R. A. M. 1999: Vigilance in wild thomasi langurs (*Presbytis thomasi*): the importance of infanticide risk. *Behav. Ecol. Sociobiol.* **45**, 137–150.
- Steiner, U. K. & Pfeiffer, T. 2007: Optimizing time and resource allocation trade-offs for investment into morphological and behavioral defense. *Am. Nat.* **169**, 118–129.
- Stone, A. I. 2007: Age and seasonal effects on predator-sensitive foraging in squirrel monkeys (*Saimiri sciureus*): a field experiment. *Am. J. Primatol.* **69**, 127–141.
- Wallage-Drees, J. M. 1989: A field study of seasonal changes in circadian activity of rabbits. *Z. Säugetierk.* **54**, 22–30.
- Winnie, J. & Creel, S. 2007: Sex-specific behavioural responses of elk to spatial and temporal variation in the threat of wolf predation. *Anim. Behav.* **73**, 215–225.
- Zullinger, E. M., Ricklefs, R. E., Redford, K. H. & Mace, G. M. 1984: Fitting sigmoidal equations to mammalian growth curves. *J. Mammal.* **65**, 607–636.