

# Animal temperament and human disturbance: Implications for the response of wildlife to tourism

J.G.A. Martin<sup>a,b,\*</sup>, D. Réale<sup>a</sup>

<sup>a</sup> Canada Research Chair in Behavioural Ecology, Groupe de Recherche en Écologie Comportementale et Animale, Université du Québec à Montréal, Département des Sciences Biologiques, BP 8888 Succursale Centre-ville, Montréal, Québec H3C 3P8, Canada

<sup>b</sup> Département de Biologie, Université de Sherbrooke, Sherbrooke, Québec J1K 2R1, Canada

Received 11 October 2006; received in revised form 16 May 2007; accepted 11 June 2007

## Abstract

Studies on the response of wildlife to human disturbance generally focus on demographic changes or on physiological and behavioural modifications directly related to stress response. Yet fewer studies have explored whether the distribution of individual animals in response to human disturbance is influenced by temperament. Temperament represents the consistency of responses of individuals in reaction to novel or challenging situations. Individuals are thus assumed to express highly consistent behaviour-hormonal response under specific stress conditions. In this study, we investigate the relations between exploration, grooming–scanning continuum, emotionality, and docility of individual Eastern chipmunks (*Tamias striatus*) and location of their burrow respective to frequentation by humans. We then assess the relationship between cortisol accumulated in the hair and both temperament and frequentation by humans. Explorative or docile chipmunks were more common in frequented areas. Hair cortisol increased with docility, but was not related to human frequentation. These results indicate that temperament may cause animals to distribute themselves in a non-random way in response to human disturbance. Integrating temperament into studies of the stress response of wildlife to humans could therefore help us understand the impact of tourism on wildlife.

© 2007 Elsevier B.V. All rights reserved.

**Keywords:** Eastern chipmunk; Hair cortisol; Hole-board test; Temperament trait; Tourism exposure

## 1. Introduction

Watching wildlife has become a popular recreational activity worldwide, with the number of participants steadily increasing (Giannecchini, 1993). Numerous studies have documented effects of ecotourism activities on wildlife behaviours such as increased habituation, decreased feeding time, hormonal changes, increased predation, decreased survivorship or reproductive success, and changes in the social and mating system (e.g. beluga whales, Blane and Jaakson, 1994; Asian rhinos, Lott and McCoy, 1995; Magellanic penguins, Fowler, 1999; marine iguanas, Romero and Wikelski, 2002; Cuban rock iguana, Lacy and Martins, 2003).

Studies of behavioural and physiological modification in free-ranging animals exposed to human perturbation have emerged (Fowler, 1999; Romero and Wikelski, 2002; Walker et al., 2005), along with a growing interest in the individual-

based approach in conservation (McDougall et al., 2006). The fact that stress is induced by human disturbance on animals is now widely accepted (Carney and Sydeman, 1999; Fowler, 1999; Dyck and Baydack, 2004). Yet few studies have investigated how temperament affects the way that individuals respond to human disturbance (McDougall et al., 2006). Temperament is defined as individual consistency in behaviour over time and across situations (Réale et al., 2007; McDougall et al., 2006), and behavioural temperament differences are highly associated with specific endocrinal responses (Buss et al., 1987; Groothuis and Carere, 2005). According to Koolhaas et al. (1999), reactive (i.e. docile, and non-explorative) animals show higher cortisol release in response to a stress than do proactive individuals (i.e. active, non-docile, and highly explorative). Furthermore, the exploration profile of an individual affects its dispersal (Fraser et al., 2001; Dingemanse et al., 2003). Therefore, depending on temperament, individuals within a population may vary in their potential to occupy areas with different levels of human perturbation. As a consequence, endocrinal differences between animals occupying disturbed and undisturbed areas may not be solely a direct effect of stress response to disturbance by humans,

\* Corresponding author. Tel.: +1 819 821 8000 62067; fax: +1 819 821 8049.  
E-mail address: [julien.martin2@usherbrooke.ca](mailto:julien.martin2@usherbrooke.ca) (J.G.A. Martin).

but may also reflect the non-random spatial distribution of individuals of different temperaments. Humans perturbation could be considered as a whole group of factors, including direct contacts, proximity, potential stressful situations and indirect effects such as food abundance and distribution, predator abundance. We decided to focus on intensity of human frequentation which is highly correlated with those factors.

In this paper, we examine the distribution of individual eastern chipmunks (*Tamias striatus*) across a human frequentation gradient in relation to their temperament, and we analyze the effects of temperament and frequentation on individual stress response. The eastern chipmunk is a common, charismatic rodent distributed across eastern North America. In the Gault Nature Reserve (Canada), a UNESCO Biosphere reserve, eastern chipmunks have been in prolonged contact with tourists, and often fed by them, for several decades. In a previous study, we have shown strong individual consistency in exploration, grooming–scanning, emotionality and docility in that population and no between-individual variations in habituation to repeated tests (Martin and Réale, 2007). Here we first investigate the relationship between chipmunk exploration, grooming–scanning, emotionality, and docility and the level of human disturbance around their burrow. We then examine the effects of temperament and human disturbance on stress response by analyzing cortisol accumulation in hair as an index of chronic stress. We finally discuss the implication of temperament and stress response for studies on the impact of human disturbance on wildlife.

## 2. Materials and methods

### 2.1. Study area and model species

Field work was conducted in the public area of the Gault Nature Reserve at Mont-Saint-Hilaire, Québec, Canada (45.5°N, 73.1°W), from May 2 to September 22, 2004. This study area consists of mature hardwood forest dominated by sugar maple (*Acer saccharum*), American beech (*Fagus grandifolium*) and red oak (*Quercus rubra*).

Chipmunks are ground-dwelling, diurnal rodents (Elliott, 1978), and their period of most intense above-ground activity (April–October) corresponds to the period of highest activity by humans (Gault Nature Reserve, personal communication). Chipmunks occupying the most frequented zone of the Reserve can hardly avoid daily contacts with humans. Furthermore, they are habituated by the presence of people. Chipmunks spend more than 90% of their time in a 40-m radius surrounding their burrow entry (Elliott, 1978; Burke Da Silva et al., 2002). We will refer to this area as a chipmunk home range hereafter. Chipmunk home ranges overlap extensively, but areas close to burrows are actively defended and there is a strong space-related dominance (Elliott, 1978).

Chipmunks were live-trapped with Sherman traps baited with sunflower seeds, sexed, weighed, ear-tagged (National Band and Tag Co., New-Port, Kentucky) and fur-clipped for identification at distance (Elliott, 1978; Giraldeau et al., 1994). We identified the burrow of 24 chipmunks, all of whom had their burrows

within an area of 50 ha near the lake shore. Although some chipmunks were already marked from studies done prior to 2004, due to a lack of complete long-term information, chipmunks could not be aged precisely. We therefore considered two categories: individuals captured prior to 2004 and individuals captured for the first time in 2004. These two categories could represent age difference or residents *versus* new immigrants.

### 2.2. Human frequentation and chipmunk density

The annual number of visitors has dramatically increased during the last decade to reach 170,000 in 2004 (Gault Nature Reserve, personal communication). The area is covered by a network of public trails, but the reserve regulation restricts people to using only trails. Frequentation by humans in a chipmunk's territory could be measured in two ways: the number of trails crossing the territory and amount of human activity on the trails. The study area was separated into two zones according to the level of human activity. The zone of high frequentation, the most frequented by the public, includes a picnic area on a lakeshore and is characterized by the highest density of trails. In the zone of low frequentation, the public only uses a few trails leading to viewpoints on summits. During summer and fall, it is common to observe between 10 and 120 people present at any given time within the zone of high frequentation (Gault Nature Reserve, personal communication). Conversely, less than 10 people per hour were observed walking on trails on week days (maximum 30 people/h during the weekend) in the low-frequentation zone (Gault Nature Reserve, personal communication). To differentiate the two zones, we attributed a score of zero or one to the zone of low and of high frequentation, respectively. Within each zone, human frequentation varied according to the density of trails. We then calculated the number of trails crossing a chipmunk's home range. In the low-frequentation zone, a maximum of one trail crossed a home range, whereas up to three trails could cross a home range in the zone of high frequentation. By summing the score of the zone and the number of trails crossing a home range, we obtained a frequentation index, ranging from zero to four, where zero represented the lowest level of frequentation (i.e. a chipmunk in the zone of low frequentation with no trails crossing their home range, and four represented the highest level of potential frequentation by humans measured in our study (i.e. a chipmunk located in the zone of high frequentation, with three trails crossing its home range).

For each chipmunk, we also calculated an index of neighbour density by counting the number of home ranges that overlapped with the home range of a given chipmunk. We defined two different categories of density: lone individuals and individuals with at least one neighbour's home range overlapping with their home range (range: 1–2).

### 2.3. Behavioural observations and temperament traits

During the summer of 2004, we performed multiple hole-board tests (average number of tests per individual = 3.7; range = 2–5) and handling bag tests (average number of tests

per individual = 5.7; range = 2–10) to determine the temperament profile of 24 individual chipmunks. The hole-board is a derivative of the open-field apparatus, with holes in the floor (File and Wardill, 1975). The hole-board was constructed from a white rectangular plastic box (80 cm × 40 cm × 40 cm) with a plexiglass top and an entrance lock on one of the longer sides. There were four holes on the floor equidistant from the entrance lock, each 5 cm in diameter and 4 cm deep. Two holes were in the center and two in the corners of the box at 15 and 5 cm from the nearest wall, respectively. The test measures the behaviour of an animal in a novel environment from which escape is prevented by a surrounding wall (Walsh and Cummins, 1976). To limit an effect of cumulative stress with repeated tests (Paz-Viveros et al., 1997), a minimum of 10 days separated two successive tests on the same individual (mean = 16 days; range = 10–20).

We measured the latency to enter the apparatus, and the duration (frequency) of scanning, grooming, rearing, climbing, head-dipping, ambulating, defecating and urinating while in the hole-board apparatus. In a principal component analysis, the first component represented an exploration index (i.e. locomotion, rearing, climbing and head-dipping), the second component a grooming–scanning continuum (with low value indicating high grooming and high scanning), and the third component an emotionality index (i.e. defecation and latency to enter the apparatus) (Martin and Réale, 2007).

Measures of an individual's reaction toward human presence (Korhonen et al., 2002; Réale et al., 2000) or to a restraint stress (Heiblum et al., 1998) are often used as a docility index (also called tameness; see McDougall et al., 2006). A handling bag test was performed to measure behavioural response to human presence and manipulation. Immediately after its release from the trap, the chipmunk was suspended in a handling bag for 1 min and the proportion of time spent immobile was used as a measure of docility.

## 2.4. Hormonal analysis

We measured cortisol accumulation in the hair as a measure of chronic stress during the period of hair growth. This method has been applied with success to measure cortisol (e.g. Koren et al., 2002; Raul et al., 2004; Davenport et al., 2006) and testosterone concentration (Koren et al., 2002, 2006). Hair was collected by fur-clipping the rump of 23 individuals in May–June and in August–September. Chipmunks show two molting peaks (i.e. early summer and late fall), although it is still controversial whether each individual molts twice a year or only once (Snyder, 1982). At Mont-Saint-Hilaire, six chipmunks that had been fur-clipped in September 2003 (i.e. late after their summer molt) had their fur grown back and were clipped again in May and in September 2004, suggesting that all individuals molted at each peak. The amount of cortisol found in the hair represents the overall accumulation during hair growth (Yang et al., 1998; Koren et al., 2002). Therefore, hair sampled in May–June (i.e. spring hair) represented cortisol accumulation in hair during winter, when chipmunk above-ground activity and frequentation by tourists of the reserve were low. Hair

sampled in August–September (i.e. summer hair) represented cortisol accumulation in hair during summer, when chipmunk above-ground activity and frequentation by tourists were high.

For extraction, we used the Yang et al. (1998) protocol. For each animal, 15–40 mg of hair was cut into pieces of 3–4 mm. Hair pieces were mixed with 2 ml of ether in a test tube, vortexed for 1 min, and then left for 1 h. The extracted solution was transferred into another test tube. One milliliter of ether was added into the original test tube and the above step was repeated. The two solutions were mixed and dried with a vacuum pump. Each sample was reconstituted with 0.1 ml of phosphate buffer solution (PBS PH = 7.0).

Each sample was dispensed into the appropriate polyclonal hormone antiserum coated well of the ELISA (solid phase enzyme linked immunoassay) microplate, in duplicates. We measured the hormone levels in the samples, using Cortisol Correlate-EIA™ kits from Assay Designs (Ann Arbor, MI, USA), according to the manufacturer's protocols. Briefly, conjugate and antibody were added to each well and the microplate was incubated for 2 h at room temperature, on a plate shaker at 50 rpm. The microplate was then washed, substrate solution added, and the plate incubated 1 h without shaking. The absorbance was read at 405 nm, just after adding stop solution. From the standard curve, we calculated the concentration of hormone in samples first in picogram per milliliter and then transformed it into picogram per milligram hair. All standards and reagents were provided by the kit.

The manufacturer's protocol indicates cross-reactivity of the antibody and the following steroids: prednisolone 122.35%; corticosterone 27.68%; 11-deoxycortisol 4.0%; progesterone 3.64%; prednisone 0.85%; testosterone 0.12%; androstenedione <0.1%; cortisone <0.1%; estradiol <0.1%. The limit of detection for the procedure is 56.72 pg/ml. Intra- and inter-assay coefficients of variation were 7.3 and 8.6, respectively.

## 2.5. Statistical analyses

### 2.5.1. Individual behavioural profile

First, we used a principal component analysis (PCA) on the correlation matrix of behaviour variables in the hole-board test to illustrate the relationship between behaviour variables, and to reduce the number of behaviour variables prior to additional statistical analyses. Then, linear mixed models of behaviours were performed using date, hour, trial order, sex, capture year, and weight as fixed effects and chipmunk identity as a random effect. Best linear unbiased predictors (BLUPs) for random effects were used as predictors of individual behaviour profiles. BLUP method provides prediction of random effects independent of other terms within a model, standardized to a mean of zero (Kruuk, 2004). They also have the advantage of being less sensitive to extreme values within data than separate regression estimates (Pinheiro and Bates, 2000). Therefore, BLUPs provide more appropriate estimates of the behaviour profile of an individual than the mean of all the measures for that individual.

Table 1

Partial spearman correlation between eastern chipmunk temperament traits and human frequentation index and neighbour density, at Mont-Saint-Hilaire, Quebec, Canada

	Exploration	Grooming–scanning	Emotionality	Docility
Frequentation index <sup>a</sup>	<b>0.46**</b>	0.10	0.15	<b>0.39*</b>
Neighbour density <sup>b</sup>	0.17	<b>−0.58**</b>	−0.07	0.04

Critical value of  $r_s$  for 21 degree of freedom is 0.37. Significant values are in bold (\* $p > 0.05$ ; \*\* $p > 0.01$ ).

<sup>a</sup> Controlled for neighbour density.

<sup>b</sup> Controlled for frequentation index.

### 2.5.2. Impact of tourism

The impact of tourism exposure on behaviour was evaluated using non-parametric tests. We estimated partial Spearman rank correlations between behaviour, frequentation index and neighbour density for each of the four behavioural variables (i.e. exploration, grooming–scanning, emotionality and docility).

Hair cortisol levels were log-transformed to normalize the data. We compared hair cortisol levels for the same animals sampled in May–June and in August–September using a paired  $t$ -test. The effect of behavioural indices, chipmunk density, and frequentation on hair cortisol, were assessed using linear regression for the two sampling periods. Statistical analyses were performed with R 2.2.0 (Ihaka and Gentleman, 1996).

## 3. Results

The temperament traits (exploration, grooming–scanning continuum, emotionality and docility) were not correlated ( $r < 0.25$  and  $P > 0.42$  for all pairwise correlations). Exploration and docility were positively and significantly related to the frequentation index (Table 1). Chipmunks with a burrow in highly frequented areas showed higher exploration scores in the hole-board and moved less in the handling bag (i.e. higher docility) than chipmunks located in areas of low frequentation (Fig. 1). The frequentation index was not related to emotionality (i.e. defecation and latency to enter the apparatus) or to the grooming–scanning continuum. Neighbour density had no significant effect on exploration, emotionality and docility (Table 1). Grooming–scanning continuum was negatively correlated with neighbour density (Table 1); chipmunks with neighbours groomed and scanned more (low value on the grooming–scanning continuum) than lone chipmunks in a hole-board situation.

Hair cortisol concentration was significantly higher in summer than in spring samples (paired  $t$ -test:  $t_7 = -2.61$ ,  $P = 0.034$ ) (Fig. 2). None of the temperament variables, age, frequentation index, or chipmunk density affected spring hair cortisol (all  $P > 0.14$ ). Cortisol concentration in summer decreased significantly with age ( $F_{1,9} = 7.19$ ,  $P = 0.025$ ) and increased significantly with docility ( $F_{1,9} = 6.29$ ,  $P = 0.033$ ) (Fig. 3), but was not significantly affected by exploration, grooming–scanning, and emotionality, or by human frequentation and neighbour density (all  $P > 0.24$ ). Removing temperament data from the model did not change the relationships between cortisol and frequentation ( $P = 0.49$ ) or chipmunk density ( $P = 0.90$ ).

## 4. Discussion

### 4.1. Behavioural observations

Chipmunks were not distributed randomly with respect to human frequentation; more explorative and more docile individuals occupied home ranges in the most frequented area. This non-random distribution might be explained in two ways: (1) chipmunks could occupy areas varying in their level of frequentation because of their intrinsic differences in temperament,

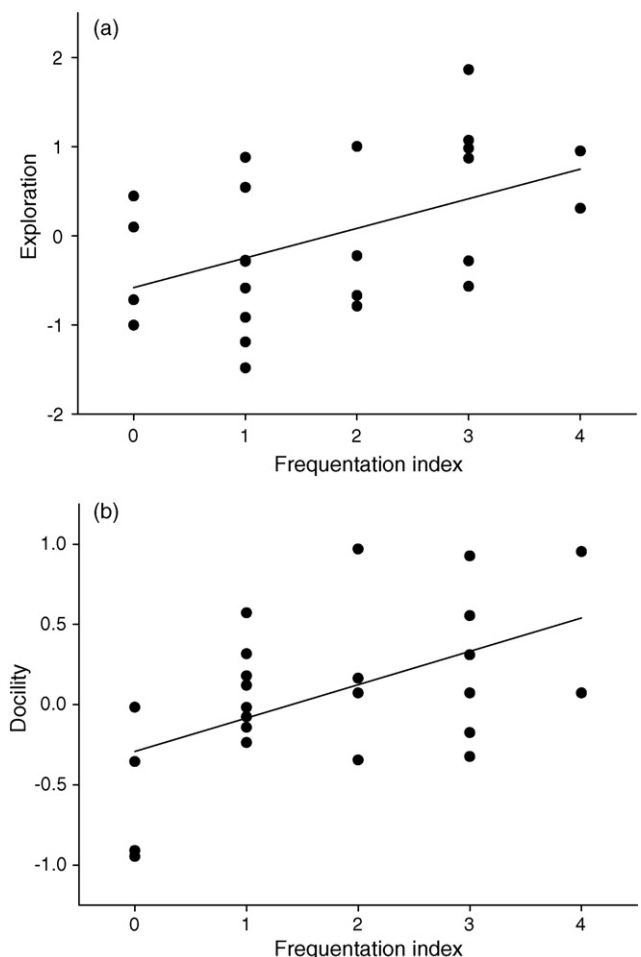


Fig. 1. Eastern chipmunk exploration (a) and docility (b) as a function of frequentation by humans, at Mont-Saint-Hilaire, Quebec, Canada. Each dot represents an individual. Human frequentation was measured using the number of trails crossing a chipmunks' home range and the level of human activity on these trails. Individual values for exploration and docility are provided using the best linear unbiased predictors.



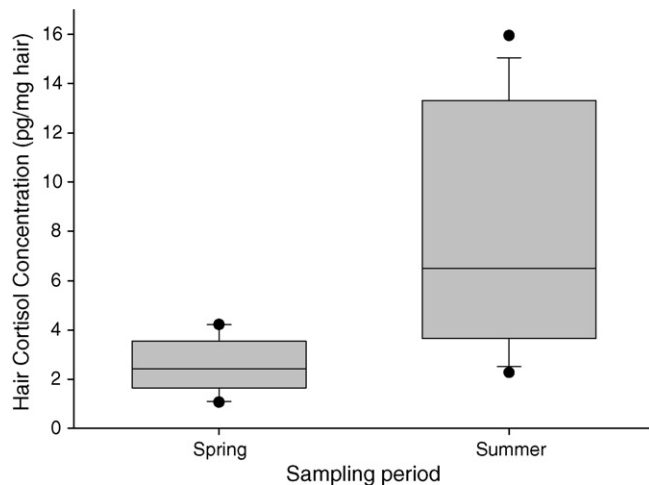


Fig. 2. Hair cortisol concentration (mean 95% confidence interval and standard error) of eastern chipmunks during spring and summer 2004 at Mont-Saint-Hilaire, Quebec, Canada. Cortisol concentration in the hair is used as an index of long-term activity of the hypothalamic–pituitary–adrenocortical system. Hair was sampled in May–June (i.e. hair growth following late fall molting peak;  $N=16$ ) and August–September (i.e. hair growth following summer molting peak;  $N=17$ ).

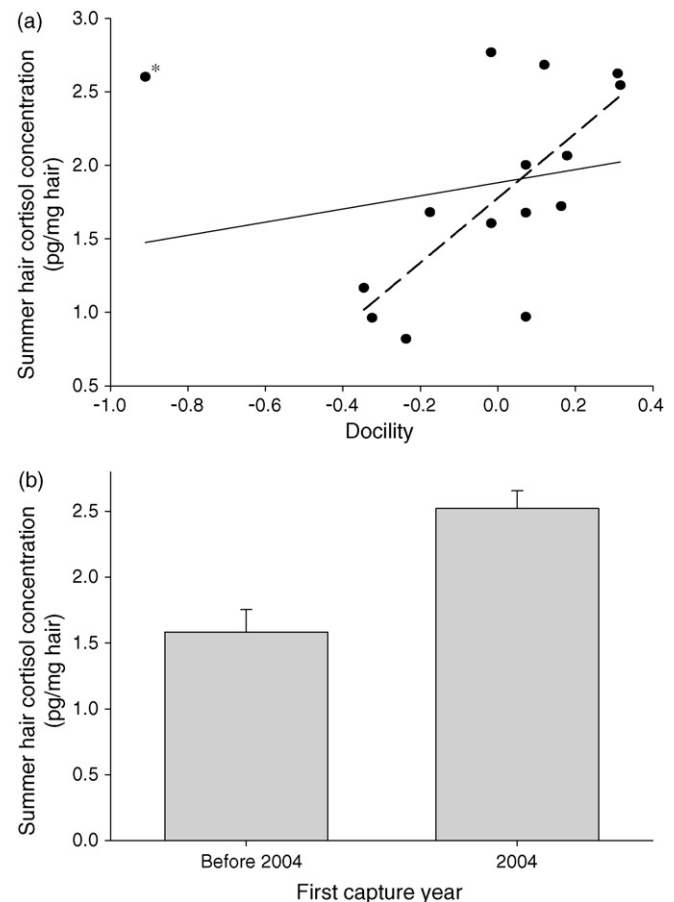


Fig. 3. Variation of (log-transformed) summer hair cortisol concentration with docility and first capture year, in eastern chipmunks at Mont-Saint-Hilaire, Quebec, Canada. (a) Regression of hair cortisol as a function of docility. Each dot represents an individual. Excluding the  $\bullet^*$  point increase the relationship (with  $\bullet^*$   $P=0.033$ ; without  $\bullet^*$   $P=0.003$ ). Solid line represents relation considering all data, and dash line when  $\bullet^*$  is excluded. (b) Mean value ( $\pm$ S.E.) of summer hair cortisol concentration for chipmunks first captured in 2004 ( $N=8$ ) or in a previous year ( $N=16$ ).

#### 4.2. Hormonal measures

Cortisol concentration was higher in summer hair (i.e. hair growth following summer molting peak) compared to spring hair (hair growth following late fall molting peak). Spring hair cortisol concentration was not linked to any environmental or behavioural variables, although the low variance in cortisol levels for spring hair limits the power of our test to detect potential effects. Increases in hair cortisol levels during summer could reflect an intrinsic seasonal variation in glucocorticosteroids in chipmunks (Kenagy and Place, 2000) resulting from a higher activity level during summer than during winter. Furthermore, chipmunks experienced less perturbation during winter than during summer. Chipmunks get in their burrow by the end of September–early October and emerge from hibernation by the end of April–early May and spend most of their time in their burrow before that period (Elliott, 1978). High summer above-ground activity in chipmunks probably translates to a higher exposure to stressful situations such as human perturbation, predator attacks, and conspecific aggression during that period.

and (2) chipmunks could show different temperaments because they experienced different levels of human frequentation during ontogeny or over recent months. According to the first hypothesis, an animal could select its home range according to its temperament. In two other species, dispersal and habitat selection for an individual are influenced by its propensity to explore (Fraser et al., 2001; Dingemanse et al., 2003). Temperament traits such as exploration or docility often show significant heritabilities (i.e. ranging from 0.22 to 0.41, Dingemanse et al., 2002; see also Gershenfeld and Paul, 1997; Koolhaas et al., 1999). This means that inter-individual variation in temperament traits has a genetic basis despite a potential plasticity (i.e. an individual can modulate its behaviour by learning and habituation). With the second hypothesis, a chipmunk that settles in a frequented area could get habituated to humans and become more explorative and more docile than a chipmunk that settles in an undisturbed area. In a previous study, we have found that whatever their location, chipmunks decreased docility when they were repeatedly tested in the handling bag (Martin and Réale, 2007). This result is not consistent with the second hypothesis and suggests that docility should decrease in areas highly frequented by humans. It is worth noting that our individual docility profile (i.e. the BLUP of docility) was corrected for the effect of repeated handling bag tests, and therefore the variation in docility among chipmunks could not be caused by the difference in the number of tests they experienced. Distinguishing between these two explanations is difficult without examining temperament and dispersal patterns of individuals marked as juveniles on their natal home range, and further studies will be needed. However, whatever the causes of this relation between temperament and human disturbance, the existence of such a distribution of temperament with frequentation could have important implications for conservation studies (see below, and for a detailed discussion see McDougall et al., 2006).

Human frequentation did not affect summer hair cortisol level, suggesting that it was not the main factor responsible for the stress of chipmunks (see below), and other factors such as intra-specific aggression, predation, or captures and manipulations might play a role in cortisol secretion. Summer hair cortisol concentration was positively related with docility, suggesting that high docility in chipmunks would correspond to a reactive coping style (*sensu* Koolhaas et al., 1999). However, contrary to Koolhaas et al. (1999), we could not find any relationship between docility and exploration, even after adjusting for the effect of human frequentation. Such association between temperament and cortisol or corticosterone release has been found in several taxa (monkeys, Cavigelli, 1999; birds, Carere et al., 2003; rodents, Sgoifo et al., 1996; Koolhaas et al., 1999; Veenema et al., 2003), indicating that temperament variables should be taken into account when comparing hormonal differences in studies of stress response to human perturbation.

Chipmunks captured for the first time in 2004, potentially juveniles or new immigrants in the study area, showed higher cortisol accumulation in the hair than those captured in previous years. Thus, the effect of first capture on cortisol accumulation could be interpreted as an age effect, or as an effect of habituation to human disturbance or to other stressful situations such as predation. The exact mechanisms of habituation, however, are unknown (Romero and Wikelski, 2002). The effects of capture and manipulation on chipmunk behaviour and cortisol levels could be rejected because we did not find a significant relationship between the number of times an individual was captured and the level of cortisol in the hair or the behaviours measured (all  $r < 0.40$ ,  $P > 0.20$ ).

Our results do not permit us to say that chipmunks in frequented areas were more stressed than those located in zones of low frequentation. The absence of a relationship between human frequentation and hair cortisol could reveal the absence of impact of humans on stress in eastern chipmunks. Alternatively, it could result from habituation to human activity in the frequented area (Fowler, 1999; Romero and Wikelski, 2002). Finally, hair cortisol may not be a sensitive method to detect stress response (Buchanan and Goldsmith, 2004). Our use of hair cortisol as a measure of stress should be considered as exploratory, and we found variation in hair cortisol with season, docility and year of first capture. Hair cortisol is a promising method for the non-invasive study of stress in wildlife for conservation purpose.

## 5. Conclusion

Using an individual-based method, we have adopted an original approach to study the impact of human disturbance on wildlife and have pointed out an important issue: individuals are distributed non-randomly according to their temperament across a human frequentation gradient. Furthermore, we have found that cortisol level in the hair was related to temperament and not to frequentation by humans. Ignoring variation in temperament of individuals when analyzing the stress response of wildlife to human disturbance may thus lead to biased conclusions. This could happen especially when comparing two groups originating from a perturbed and an undisturbed area, like most of studies

on human impact. Endocrinal response of each of these groups may result from specific stress responses associated with the temperament of individuals occupying the different areas. In the absence of knowledge on animal temperament, tourism impact could be under- or overestimated. Animal temperament may thus be considered in future studies on human impact on wildlife.

## Acknowledgements

Thanks to Gault Nature Research Center and the McGill University field station at Mont-Saint-Hilaire for authorization to work and help in the field. We are grateful to Vincent Lefebvre for his help in field work. We thank Catherine Mounier for letting us using her lab facilities and for providing advices on ELISA protocol. We thank Frank Cézilly and two anonymous reviewers for their help in improving the paper. Thanks to Luc-Alain Giraldeau, Catherine Jumarie and the members of the Groupe de Recherche en Écologie Comportementale et Animale for providing advices and exchanging ideas throughout the study, and to Bill Vickery, Eric Lucas, and Carolyn Hall, who provided fruitful comments on an earlier draft of the manuscript. J.M. was supported by a FARE-UQAM fellowship from the UQAM Foundation and a Hydro-Québec Fellowship from Hydro-Québec and UQAM Foundation. Natural Sciences and Engineering Council of Canada and the Canadian Foundation for Innovation provided financial support to D.R.

## References

- Blane, J.M., Jaakson, R., 1994. The impact of ecotourism boats on the St-Lawrence beluga whales. *Environ. Conserv.* 21, 267–269.
- Buchanan, K.L., Goldsmith, A.R., 2004. Noninvasive endocrine data for behavioural studies: the importance of validation. *Anim. Behav.* 67, 183–185.
- Burke Da Silva, K., Mahan, C., Da Silva, J., 2002. The trill of the chase: eastern chipmunks call to warn kin. *J. Mammal.* 83, 546–552.
- Buss, A.H., Chess, S., Goldsmith, H., Hinde, R., McCall, R., Plomin, R., Rothbart, M., Thomas, A., 1987. What is temperament: four approaches. *Child Dev.* 58, 505–529.
- Carere, C., Groothuis, T.G.G., Möstl, E., Daan, S., Koolhaas, J.M., 2003. Fecal corticosteroids in a territorial bird selected for different personalities: daily rhythm and the response to social stress. *Horm. Behav.* 43, 540–548.
- Carney, K.M., Sydeman, W.J., 1999. A review of human disturbance effects on nesting colonial waterbirds. *Waterbirds* 22, 68–79.
- Cavigelli, S.A., 1999. Behavioural patterns associated with faecal cortisol levels in free-ranging female ring-tailed lemurs *Lemur catta*. *Anim. Behav.* 57, 935–944.
- Davenport, M.D., Tienfenbacher, S., Lutz, C.K., Novak, M.A., Meyer, J.S., 2006. Analysis of endogenous cortisol concentrations in the hair of rhesus macaques. *Gen. Comp. Endocrinol.* 147, 255–261.
- Dingemanse, N.J., Both, C., Drent, P.J., Van Oers, K., Van Noordwijk, A.J., 2002. Repeatability and heritability of exploratory behaviour in great tits from the wild. *Anim. Behav.* 64, 929–938.
- Dingemanse, N.J., Both, C., Van Noordwijk, A.J., Rutten, A.L., Drent, P.J., 2003. Natal dispersal and personalities in great tits (*Parus major*). *Proc. R. Soc. Lond. Ser. B Biol. Sci.* 270, 741–747.
- Dyck, M.G., Baydack, R.K., 2004. Vigilance behaviour of polar bears (*Ursus maritimus*) in the context of wildlife-viewing activities at Churchill, Manitoba, Canada. *Biol. Conserv.* 116, 343–350.
- Elliott, L., 1978. Social Behavior and Foraging Ecology of the Eastern Chipmunk (*Tamias striatus*) in the Adirondack Mountains. Smithsonian Institution Press, Washington.

- File, S.E., Wardill, A.G., 1975. Validity of head-dipping as a measure of exploration in a modified hole-board. *Psychopharmacologia* 44, 53–59.
- Fowler, G.S., 1999. Behavioral and hormonal responses of magellanic penguins (*Spheniscus magellanicus*) to tourism and nest site visitation. *Biol. Conserv.* 90, 143–149.
- Fraser, D.F., Gilliam, J.F., Daley, M.J., Le, A.N., Skalski, G.T., 2001. Explaining leptokurtic movement distributions: intrapopulation variation in boldness and exploration. *Am. Nat.* 158, 124–135.
- Gershenfeld, H.K., Paul, S.M., 1997. Mapping quantitative trait loci for fear-like behaviors in mice. *Genomics* 46, 1–8.
- Giannacchini, J., 1993. Ecotourism: new partners, new relationships. *Conserv. Biol.* 7, 429–432.
- Giraldeau, L.-A., Kramer, D.L., Deslandes, I., Lair, H., 1994. The effect of competitors and distance on central place foraging eastern chipmunks, *Tamias striatus*. *Anim. Behav.* 47, 621–632.
- Groothuis, T.G.G., Carere, C., 2005. Avian personalities: characterization and epigenesis. *Neurol. Biobehav. Rev.* 29, 137–150.
- Heiblum, R., Aizenstein, O., Gvoryahu, G., Voet, H., Robinson, B., Snapir, N., 1998. Tonic immobility and open field responses in domestic fowl chicks during the first week of life. *Appl. Anim. Behav. Sci.* 60, 347–357.
- Ihaka, R., Gentleman, R., 1996. R: a language for data analysis and graphics. *J. Comp. Graph. Stat.* 5, 299–314.
- Kenagy, G.J., Place, N.J., 2000. Seasonal changes in plasma glucocorticosteroids of free-living female yellow-pine chipmunks: effects of reproduction and capture and handling. *Gen. Comp. Endocrinol.* 117, 189–199.
- Koolhaas, J.M., Korte, S.M., De Boer, S.F., Van Der Vegt, B.J., Van Reenen, C.G., Hopster, H., De Jong, I.C., Ruis, M.A.W., Blokuis, H.J., 1999. Coping styles in animals: current status in behavior and stress physiology. *Neurosci. Biobehav. Rev.* 23, 925–935.
- Koren, L., Mokady, O., Karasov, T., Klein, J., Koren, G., Geffen, G., 2002. A novel method using hair for determining hormonal levels in wildlife. *Anim. Behav.* 63, 403–406.
- Koren, L., Mokady, O., Geffen, E., 2006. Elevated testosterone levels and social ranks in female rock hyrax. *Hormon. Behav.* 49, 470–477.
- Korhonen, H.T., Jauhiainen, L., Rekila, T., 2002. Effect of temperament and behavioural reactions to the presence of a human during the pre-mating period on reproductive performance in farmed mink (*Mustela vison*). *Can. J. Anim. Sci.* 82, 275–282.
- Kruuk, L.E.B., 2004. Estimating genetic parameters in natural populations using the ‘animal model’. *Philos. Trans. R. Soc. B* 359, 873–890.
- Lacy, K.E., Martins, E.P., 2003. The effect of anthropogenic habitat usage on the social behaviour of a vulnerable species *Cyclura nubila*. *Anim. Conserv.* 6, 3–9.
- Lott, D.F., McCoy, M., 1995. Asian rhinos *Rhinoceros unicornis* on the run? Impact of tourist visits on one population. *Biol. Conserv.* 73, 23–26.
- Martin, J.G.A., Réale, D., 2007. Temperament, risk assessment and habituation to novelty in eastern chipmunks, *Tamias striatus*. *Anim. Behav.*, in press.
- McDougall, P.T., Réale, D., Sol, D., Reader, S.M., 2006. Wildlife conservation and animal temperament: causes and consequences of evolutionary change for captive, reintroduced, and wild populations. *Anim. Conserv.* 9, 39–48.
- Paz-Viveros, M., Martin, S., Martin, M.I., 1997. Methodological aspects about the combination of holeboard, plus-maze and open-field within a test battery, in ethopharmacological studies. *Sci. Technol. Anim. Lab.* 22, 171–175.
- Pinheiro, J.C., Bates, D.M., 2000. *Mixed-Effects Models in S and S-Plus*. Springer-Verlag, New York.
- Raul, J.S., Cirimele, V., Ludes, B., Kintz, P., 2004. Detection of physiological concentrations of cortisol and cortisone in human hair. *Clin. Biochem.* 37, 1105–1111.
- Réale, D., Gallant, B.Y., Leblanc, M., Festa-Bianchet, M., 2000. Consistency of temperament in bighorn ewes and correlates with behaviour and life history. *Anim. Behav.* 60, 589–597.
- Réale, D., Reader, S.M., Sol, D., McDougall, P., Dingemanse, N., 2007. Integrating animal temperament within ecology and evolution. *Biol. Rev.* 82, 291–318.
- Romero, L.M., Wikelski, M., 2002. Exposure to tourism reduces stress-induced corticosterone levels in Galapagos marine iguanas. *Biol. Conserv.* 108, 371–374.
- Sgoifo, A., De Boer, S.F., Haller, J., Koolhaas, J.M., 1996. Individual differences in plasma catecholamine and corticosterone stress responses of wild-type rats: relationship with aggression. *Physiol. Behav.* 60, 1403–1407.
- Snyder, D.P., 1982. *Tamias striatus*. *Mamm. Sp.* 168, 1–8.
- Veenema, A.H., Meijer, O.C., De Kloet, E.R., Koolhaas, J.M., 2003. Genetic selection for coping style predicts stressor susceptibility. *J. Neuroendocrinol.* 15, 256–267.
- Walker, B.G., Boersma, P.D., Wingfield, J.C., 2005. Physiological and behavioral differences in magellanic penguin chicks in undisturbed and tourist-visited locations of a colony. *Conserv. Biol.* 19, 1571–1577.
- Walsh, R.N., Cummins, R.A., 1976. The open-field test: a critical review. *Psychol. Bull.* 83, 482–504.
- Yang, H.Z., Lan, J., Meng, Y.J., Wan, X.J., Han, D.W., 1998. A preliminary study of steroid reproductive hormones in human hair. *J. Steroid Biochem. Mol. Biol.* 67, 447–450.