



Many eyes or many ewes: vigilance tactics in female bighorn sheep *Ovis canadensis* vary according to reproductive status

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In gregarious animals, there is usually a negative relationship between individual vigilance and group size. This effect of group size is generally explained by increasing probability of predator detection (the many-eyes hypothesis) and by the dilution of risk occurring in larger groups. Few studies have attempted to examine the specific implications of either hypothesis on the expected vigilance pattern of an animal. Here we examine whether reproductive status affects vigilance patterns in bighorn sheep *Ovis canadensis* ewes. We also test whether the observed vigilance patterns are consistent with predictions from dilution or detection models of vigilance. Although vigilance decreased with increasing group size, vigilance tactics differed between barren and lactating females. Lactating ewes relied solely on predator detection. In contrast, barren ewes benefited from both detection and dilution effects when group size increased and adjusted vigilance effort according to the proportion of lactating ewes in their group. It is generally assumed that gregariousness increases safety. Here we further show that reproductive status influenced how animals reduce predation risk and that some individuals take advantage of the vigilance effort provided by others.

The relationship between gregariousness and anti-predatory benefits is a central question in behavioural ecology (Krebs and Davies 1993). It is well established that grouping provides anti-predatory advantages (Hamilton 1971, McNamara and Houston 1992, Caro 2005). Declining individual vigilance effort with increasing group size has been widely reported for both mammals and birds (Elgar and Catterall 1981, Dehn 1990, Lima and Dill 1990, Lima 1998, Lima et al. 1999). This group size effect on vigilance is commonly explained in two ways: increased probability of detecting an approaching predator when more eyes are available for scanning (i.e. the many-eyes hypothesis: Lima 1990, 1995) and dilution of risk with each increase in group size (Pulliam 1973). However, there are few published attempts to separate the effects of detection from those of dilution (Dehn 1990, Fairbanks and Dobson 2007).

Recently, Lung and Childress (2007) reported differences in how the sexes adjusted vigilance tactics and effort according to group size in elk *Cervus elaphus*. In mixed groups of elk, adult males are only vigilant during the rut to gather information about mating opportunities while females always use their vigilance effort toward predator detection. No studies to date have tested for differences in vigilance tactics among group members of the same sex. The aim of our study is to determine whether, in a group of the same sex, individuals differ in the extent to which they

rely on detection versus dilution as a mean of reducing predation risk.

As far as we know, no study has investigated how the mechanisms of the group size effect on vigilance could differ between individuals of different reproductive status. We examine whether reproductive status can lead to individual differences in vigilance tactics in bighorn sheep *Ovis canadensis* ewes. Lambs are at higher risk of predation than adults (Hass 1989, Ross et al. 1997, Jarnemo and Liberg 2005), and mothers should therefore be more vigilant than non-mothers; early detection of an approaching threat can increase the safety of their lamb (Lipetz and Bekoff 1982, Dehn 1990). For mothers, detection should supersede dilution because it would not be beneficial for their own lamb to represent a source of dilution, whereas other lambs and group mates could indeed serve to dilute predation risk. Bighorn sheep are appropriate models to study differences in female vigilance tactics as they show strong sexual segregation outside the late autumn rut (Hogg and Forbes 1997). Ewe groups usually include yearlings, lambs and rams <5 years of age, however the proportion of males in ewe groups never exceeds 10% (Ruckstuhl and Festa-Bianchet 2001). Male vigilance tactics would therefore only minimally influence female vigilance effort and tactic use. Furthermore, lambs are not weaned before September, and mother–lamb associations are strong during the entire summer.

Each group member can enhance fitness by reducing its probability of being caught during a predator attack by relying on safety benefits provided by the presence of congeners (Williams 1964). The advantage of the detection tactic is the possibility of detecting a predator earlier during its approach. Although detection power can be increased through cooperative scanning by group members, coordinated scanning is rarely reported and unlikely to be an evolutionary stable strategy. Cooperative scanning is vulnerable to “cheaters” that could benefit from reduced predation risk without contributing to the collective vigilance effort of the group (Hamilton 1971, McNamara and Houston 1982). These individuals could reallocate saved vigilance time to other fitness enhancing activities such as foraging or mating (Pulliam et al. 1982). Expected gains in safety by cheaters may well depend on the number of individuals using that tactic in the population. As their number increases, the proportion of efficient predator detectors decreases altering de facto safety advantages provided by grouping, a situation akin to producer-scrounger games (Barnard and Sibly 1981, Giraldeau and Caraco 2000). The appearance of individuals taking advantage of the vigilance of others within a group may be more likely if some group members can only benefit from early detection while others can benefit from both early detection and increased dilution.

Here we focus on how, as group size increases, ewes adjust vigilance effort according to their reproductive status. To address this, we examine models developed by Dehn (1990) that describe effects of both dilution and detection on vigilance behaviour when group size increases. These models predict variation in individuals' scanning rate (used below as a proxy of vigilance behaviour) with respect to group size and proportion of individuals actively vigilant.

Methods

Study site and population

The study population inhabits Ram Mountain (52°N, 115°W, elevation 1082–2173 m), Alberta, Canada. Fieldwork was conducted from 2 June–3 October 1998. The population consisted of 105 individuals: 57 adult ewes, 28 rams, 4 yearlings and 19 lambs.

Since 1971, sheep on Ram Mountain have been captured in a corral trap baited with salt from the end of May to early October. All ewes were individually marked with coloured collars. Age was known for all animals and reproductive status was determined at each capture by udder examination, with ewes classified as barren or lactating. Reproductive status was also determined at each focal observation: ewes were classified as lactating if seen nursing a lamb.

Bighorn sheep are generally preyed upon by wolves *Canis lupus*, black bears *Ursus americanus*, coyotes *C. latrans*, and golden eagles *Aquila chrysaetos* (Jorgenson et al. 1997). At Ram Mountain, bighorn sheep were mostly preyed upon by cougars *Puma concolor* in ambush (Festa-Bianchet et al. 2006). In 1998, we observed two attacks, one of which was successful. Furthermore, signs near the carcasses of two 14-year-old ewes indicated cougar preda-

tion (Réale and Festa-Bianchet 2003). One wolf and three black bears were also sighted in 1998.

Behavioural observations

Groups were observed with a spotting scope (20–45×) at >300 m, a distance that avoided observer detection by animals. Group composition (identity and sex-age class of each sheep) and position were noted (UTM co-ordinates). A group was defined as an aggregation of individuals in visual contact with one another. Individuals out of visual contact were excluded because they likely could not contribute to group vigilance or inform others of danger (Metcalf 1984). Using this definition, group members were never more than 50 m from each other.

Data on vigilance behaviour were obtained with focal animal sampling (Altmann 1974); a focal individual was randomly selected from a group. All observations were specifically conducted on foraging groups. An individual was considered to be vigilant when it interrupted its foraging activities with its head raised above its shoulders (Frid 1997, Ruckstuhl et al. 2003). Observations lasted for a minimum of 300 s and were terminated at 900 s (mean = 744 s ± 208 s; n = 380). For each focal observation, we calculated the frequency of head lifts per min, hereafter referred to as scanning rate. At 30 s intervals, we noted the distance to forest cover divided into three categories: <15 m, 15–50 m, and >50 m. We also noted distance to nearest neighbour (excluding lambs). We measured distances by sheep-length units to reduce the variation in estimation error caused by observing groups at different distances. Group altitude was determined with a topographical map using the group position coordinates.

Vigilance model

We compared four models of vigilance developed by Dehn (1990) to predict the relationship between individual scanning rate and group size (Table 1): 1) Detection model, predicting the decline of individual vigilance based solely on increased early detection with group size and assuming that grouping reduces the level of individual vigilance required to maintain a given probability of predator detection, 2) Security model, that combines both changes in detection and dilution with group size and predicting the probability for a given individual to survive after an attack, 3) Security model with non-vigilant animals, the previous security model but accounting for the possibility that some group members may not be actively engaged in vigilance, though inevitably contributing to dilution, and 4) Security model with lambs and mothers, a modified model 3 to account for the proportion of females with lambs and for the probability that both mother and lamb would survive an attack through the dilution of risk.

Bighorn sheep lambs spend most of the time playing, grazing and ruminating and are very rarely vigilant (pers. obs.). In models 3 and 4 (Table 1), we consider lambs as non-actively vigilant animals and other animals (mostly adult females) as actively vigilant (Na refers to group size-number of lambs). The four vigilance models were first fitted to the complete data set to quantify the vigilance

Table 1. Vigilance models (developed by Dehn 1990). N: group size; Na: Number of animals actively vigilant (N-number of lambs); Pw: Proportion of mothers with a lamb; a_i: parameters estimates.

1. Detection model	$V = a_0 + a_1 \frac{1}{N}$
2. Security model	$V = a_0 + a_1 \frac{1}{N} + a_2 \frac{\ln(N)}{N}$
3. Security model with non-vigilant (lambs)	$V = a_0 + a_1 \frac{1}{Na} + a_2 \frac{\ln(N)}{Na}$
4. Security model with lambs and proportion of mothers	$V = a_0 + a_1 \frac{1}{Na} + a_2 \frac{\ln(N)}{Na} + a_3 \frac{Pw}{Na}$

1) Dehn (1990) considered that the probability that at least one member of a group of size N detects the predator is: $P_{GD} = 1 - e^{-V \cdot T \cdot N}$, where V is the scanning frequency of an individual and T is the time that a predator could be detected by a given prey during its uncovered approach. He also assumed P_{GD} to be constant. Solving this equation for scanning frequency, he obtained the detection model. 2) He defined security as the probability that an animal survives the risk of predation (Ps). Ps is given by the following equation

$$P_s = P[\text{survival}|\text{predator present}]P_p + P[\text{survival}|\text{predator not present}](1 - P_p) \quad (a)$$

where P_p is the probability that a predator is present. Survival can occur in two different ways when a predator is present: first by early detection (P_{GD}), and second by dilution ($\frac{N-1}{N}$). When no predators are present, the survival is considered to be one. Solving the P_s equation for vigilance, he obtained the security model. 3) Na, the number of animals actively vigilant (N-number of lambs) is included in the previous Security model. If some individuals are non-vigilant, this will affect the number of individuals involved in detection effort ($P_{GD} = 1 - e^{-V \cdot T \cdot Na}$), but will not affect dilution ($\frac{N-1}{N}$). Solving Eq. (a) with these new parameters gives model 3. 4) For a female with a lamb, to reflect the probability of both female and lamb surviving through dilution, Dehn considered dilution as $\frac{N-2}{N}$. Solving Eq. (a) for female with a lamb, he obtained $V = a_0 + a_1 \frac{1}{Na} + a_2 \frac{\ln(N/2)}{Na}$. After that he assumed that scanning rate among the group is a weighted average of females with and without offspring. The Security model with lambs and proportion of females can be expressed as model 4 where Pw is the proportion of females with a lamb.

patterns of bighorn sheep herds, then fitted separately for mother and non-mother observations.

Model selection

To determine which candidate models best explained the data for the complete group and for lactating or non-lactating ewes, we used Akaike's information criterion (AIC) (Akaike 1974, Burnham and Anderson 2002). Models were compared according to the AIC statistic, and ranked according to their normalized Akaike weights (AICw). The best model had the largest AICw and the smallest AIC statistic (Burnham and Anderson 2002). Results of the model selection process are presented following the recommendations of Burnham and Anderson (2002). We used AICc (AIC corrected for small sample size; Hurvich and Tsai 1989) to select models and our data were not overdispersed. We also compared evidence ratios: the ratio of the Akaike weight of the model with the lowest AICc score to the weight of the model of interest. Akaike weights can be interpreted as the probability that the selected model is the best if all the candidate models were to be fitted to our bighorn sheep data set, whereas evidence ratios provide evidence against a model as being the best model in the set of candidate models. The larger the evidence ratio, the stronger is the evidence against a model relative to the reference model in a pair under consideration (Burnham and Anderson 2002). In case where several candidate models had $\Delta AICc < 2.00$, suggesting a certain level of uncertainty regarding the best model, we considered the model with the lowest AICc as the best-fitting model.

Nonlinear mixed models using maximum likelihood method (ML) were conducted to fit models to the data.

Ewe identity was included in all models as a random effect to control for pseudo-replication and for inter-individual variation in vigilance. A previous study showed that vigilance in ewes varied according to altitude, distance to cover, distance to nearest neighbour (Réale et al. unpubl.). These variables were included in all models in addition to detection and dilution effects to take into account their impact on vigilance. We also compared the three best supported models to a null model (intercept + altitude + distance to cover + distance to nearest neighbour and identity of the focal individual as a random effect) using a log-likelihood ratio test. All statistical analyses were performed using R 2.4.0 (R Development Core Team).

Results

For all observations combined, the best supported model is the security model (Table 2a). Considering mothers separately from non-mothers, detection and security models have $\Delta AICc < 2$ and similar evidence ratios, 1.00 and 1.50 respectively. In spite of the level of uncertainty surrounding these two closely competing models, we consider the detection model (model 1), the model with the lowest AICc (Table 2a), as the best-fitting model suggesting that mothers rely mostly on early detection. Similarly, for non-mothers, models 3 and 4 both fit the data well ($\Delta AICc < 2$ and evidence ratios: 1.12 and 1.00) indicating that barren ewes mainly rely on early detection, risk dilution and presence of lambs, however model 4, that also accounts for the proportion of females followed by a lamb (Pw), had the lowest AICc (Table 2a). Parameter a₃ (model 4, barren ewes) includes zero within $\pm SE$ (Table 3) and thus could be

Table 2. Model selection with AIC. a) AIC value of vigilance models; b) Comparison of best-fitting models with the null model (intercept + altitude + distance to cover + distance to nearest neighbour and identity of the focal individual as a random effect). All vigilance models were fitted to three different datasets; best-fitting models are presented in bold.

	AICc	Δ AICc	w_i	Evidence ratio
a) AIC value				
Ewes group (all individuals)				
1. Detection	601.44	4.66	0.08	10.26
2. Security	596.78	0.00	0.80	1.00
3. Security with lambs (non vigilant)	609.86	13.08	0.00	693.78
4. Security with lambs and proportion of mothers	600.52	3.74	0.12	6.49
Lactating ewes				
1. Detection	200.45	0.00	0.52	1.00
2. Security	201.26	0.81	0.35	1.50
3. Security with lambs (non vigilant)	205.05	4.59	0.05	9.95
4. Security with lambs and proportion of mothers	204.28	3.83	0.08	6.79
Barren ewes				
1. Detection	416.92	3.13	0.08	4.77
2. Security	415.66	1.86	0.16	2.54
3. Security with lambs (non vigilant)	414.03	0.23	0.36	1.12
4. Security with lambs and proportion of mothers	413.80	0.00	0.40	1.00
		χ^2	DF	p value
b) Comparison to null model				
All individual: 2) Security model		100.65	2	< 0.001
Lactating ewes: 1) Detection model		27.05	1	< 0.001
Barren ewes: 4) Security model with lambs and proportion of mothers		57.83	3	< 0.001

considered non-significant. However, the addition of this parameter in model 3 (leading to model 4) improves the fit of the data. The three selected models fit the data significantly better than a null model (Table 2b). Parameter estimates are relatively similar between selected models (Table 3). Our results show a reduction in the vigilance of barren ewes as the proportion of mothers in a group increases (Table 3). In all situations, our results show a decline of scanning rate associated with an increasing group size (Fig. 1). In agreement with Réale et al. (unpubl.), individual scanning rate increases with distance to cover and to nearest neighbour but decreases with altitude. Also, ewe's identity explained a significant proportion of the variance (for all ewes: 12.7%, for mothers: 22.9% and for barren ewes only: 9.9%).

Discussion

Our results show that ewes adopt different tactics of vigilance according to their reproductive status, even though no significant difference in vigilance between barren and lactating ewes has been reported for this population (Réale et al. unpubl.). While bighorn ewes exhibit the commonly

reported response to an increase of group size by reducing their individual level of vigilance (Elgar 1989, Lima 1990), we provide evidence that reproductive status may influence how individuals obtain an anti-predatory benefit from gregariousness, and that some individuals within a group could take advantage of the vigilance efforts provided by others.

Bighorn ewes reduce their scanning rate when in large groups independently of reproductive status (Fig. 1). This result is consistent with previous studies that indicate grouping reduces predation risk (Cresswell 1994, Lima et al. 1999). A decline in scanning rate has been commonly reported (Roberts 1996, Lima et al. 1999) and it was generally explained by the safety benefits of grouping. To obtain these advantages, individuals have to respond adequately to an increased group size. Previous studies have shown that gregarious animals adjust their vigilance level according to their position within the group, group density, and activities of other group members, as well as to the distance of nearest neighbours and refuge (Frid 1997, Lima et al. 1999, Fernandez-Juricic and Kacelnik 2004, Devereux et al. 2006). Our results indicate that individuals not only adjust their vigilance level but also differ in the way they rely on both predator detection and risk dilution.

Table 3. Parameters estimates (with standard errors) of best fitted models. N: group size; Na: Number of animals actively vigilant (N-number of lambs); Pw: Proportion of mothers followed a lamb; a_i: parameters estimates.

Selected models	a ₀	a ₁	a ₂	a ₃
All ewes: 2) Security model $V = a_0 + a_1 \frac{1}{N} + a_2 \frac{\ln(N)}{N}$	0.40 (0.09)	1.44 (0.15)	0.74 (0.27)	
Lactating ewes: 1) Detection model $V = a_0 + a_1 \frac{1}{N}$	0.37 (0.34)	1.59 (0.29)	—	—
Barren ewes: 4) Security with lambs and proportion of mothers $V = a_0 + a_1 \frac{1}{Na} + a_2 \frac{\ln(N)}{Na} + a_3 \frac{Pw}{Na}$	0.37 (0.11)	1.37 (0.18)	0.66 (0.36)	-0.51 (1.09)

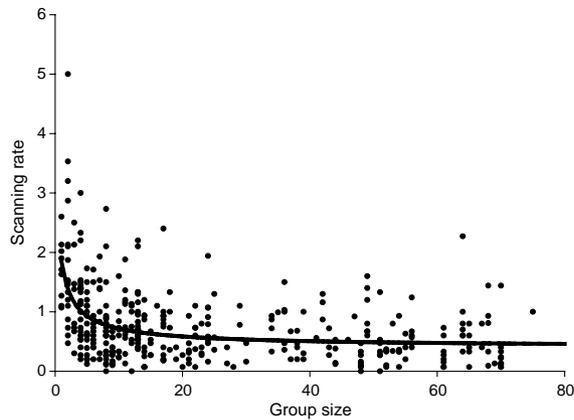


Fig. 1. Scanning rate of bighorn ewes with group size. The solid line shows the Security model (model 2) that best fitted data of bighorn ewes scanning rate in the Ram Mountain population.

When not considering phenotypic difference among ewes, the security model accounting for both dilution of risk and predator detection provides the best fit and explains our scanning rate data. This suggests that the overall decrease of bighorn ewes scanning rate with group size within the Ram Mountain population is induced by early detection and dilution. Not all group members, however, rely on both early threat detection and numerical dilution of risk. For lactating ewes, early detection of predators appears to be the main component of vigilance. On the other hand, barren ewes benefit from both detection and dilution effects when group size increases and may also adjust vigilance effort according to the proportion of lactating ewes within the group; they devote less time in vigilance in groups with high proportion of mothers.

As suggested by Williams (1964), each group member seeks to decrease its probability of being killed by a predator but also tries to improve its reproductive success. To maximize its fitness, a mother should enhance both her survival and that of its young, whereas a non-mother should only enhance her own survival. Early detection of predators would increase both mother and lamb survival. Dilution of risk would be less effective for a mother as both the mother and its young are at risk. Also, juveniles are the most vulnerable individuals (Hass 1989), and for lambs, dilution should be based only on their number in the group. Our results show neither an effect of number of lambs (Pw: proportion of mothers in the group) on vigilance of mothers nor an effect of dilution. Barren females, when aggregated with lactating ones, benefit in three ways: 1) grouping with lactating females provides an increased detection of threat, 2) the presence of lambs enhances protection because of the possible specialization of predators on the most vulnerable individuals of the group, and finally 3) non-mothers could decrease their vigilance effort because of protection gained through the coupling of the two previous effects and could reallocate this saved time to other fitness enhancing activities.

Benefits obtained by ewes without dependent young when aggregating with a high proportion of mothers reveal that vigilance effort between group mates is unequal and some individuals can use supplemental predator detection effort from others and be viewed as cheaters. If the general

pattern of vigilance is directed toward a decline of individual vigilance, which is consistent with safety benefits of gregariousness, then group members differ in the way they reach this overall safety advantage.

If gregarious animals' security is guided by both the probability that at least one member of the group detects an approaching predator and by the reduced likelihood of being killed during an attack, the former effect is thought to contribute greatly to individual security in small groups, but its contribution decreases as group size increases. Indeed, both empirical and theoretical works have shown that the dilution effect is more important in larger groups (Lima 1995) than the detection effect (Dehn 1990, reviewed by Roberts 1996). Unfortunately, these studies did not take into consideration that some individuals could be limited in their use of one or both tactics. Our findings suggest that some females never benefit from the complete security effect of being in a group; the exclusive use of the detection tactic is observed only in lactating ewes. Only barren females benefit from both effects to enhance their individual security but as group size increases the safety implications of detection become lower. Scanning may serve another purpose: monitoring other group members in order to gather information about their social status (Lung and Childress 2007), their vigilance levels (Fernandez-Juricic et al. 2004, 2005) or their foraging activities (Valone 1989, Dall et al. 2005, Shrader et al. 2007). The role of scanning in barren ewes needs to be further defined, but we lack here the information on the direction of ewes' gazes, whether toward the surrounding environment or toward congeners, in order to answer this question properly.

It is generally assumed that the fitness provided by alternative tactics depends on their frequencies in the population, i.e. frequency dependence, and fitness of an individual would be affected by the actions of others congeners (Parker 1984). Based on predictions of theoretical models dealing with frequency dependence (Parker 1984, Gross 1996, Barta et al. 1997), future works may investigate the existence of a stable point where both vigilance tactics would obtain equivalent pay-offs according to group sizes.

Despite the considerable effort invested in the study of group living benefits, few attempts have been made to examine the specific implications of both predator detection and risk dilution and the basis of individual differences used to reach the anti-predatory advantages of grouping. We believe that studies of vigilance behaviour in gregarious animals could be directed toward the coexistence of different vigilance tactics with two main objectives: distinguishing the functional interpretation of the different tactics and testing the frequency dependence use of these tactics.

Acknowledgements – We sincerely thank Bruno Gallant for providing data on vigilance. G. R. was supported by a NSERC grant to Luc-Alain Giraldeau and by a FARE UQAM Foundation grant. J. M. was supported by a NSERC grant to Marco Festa-Bianchet and by an Univ. de Sherbrooke Fellowship. Marco Festa-Bianchet, Luc-Alain Giraldeau, Jon Jorgenson, Kimberley Mathot, Joseph Nocera, Denis Réale, Stephanie Surveyer and William Vickery provided fruitful comments on earlier drafts. We also thank Adrian Shrader and Kenneth Schmidt for their help to improve this paper. The study was funded by Challenge Grants in Biodiversity Program, Dept of Biological Sciences, Univ. of

Alberta, through joint efforts of the sportsmen of Alberta and the Alberta Conservation Association.

References

- Akaike, H. 1974. A new look at statistical model identification. – IEEE Trans. Automat. Contr. 19: 716–723.
- Altmann, J. 1974. Observational study of behavior: sampling methods. – Behaviour 49: 227–267.
- Barnard, C. J. and Sibly, R. M. 1981. Producers and scroungers: a general model and its application to captive flocks of house sparrows. – Anim. Behav. 29: 543–550.
- Barta, Z. et al. 1997. Geometry for a selfish foraging group: a genetic algorithm approach. – Proc. R. Soc. B. 264: 1233–1238.
- Burnham, K. P. and Anderson, D. R. 2002. Model selection and multi-model inference – a practical information-theoretic approach (2nd ed.). – Springer.
- Caro, T. 2005. Antipredator defenses in birds and mammals. – Chicago Univ. Press.
- Cresswell, W. 1994. Flocking is an effective anti-predation strategy in redshanks, *Tringa totanus*. – Anim. Behav. 47: 433–442.
- Dall, S. R. X. et al. 2005. Information and its use by animals in evolutionary ecology. – Trends Ecol. Evol. 20: 187–193.
- Dehn, M. M. 1990. Vigilance for predators: detection and dilution effects. – Behav. Ecol. Sociobiol. 26: 337–342.
- Devereux, C. L. et al. 2006. Predator detection and avoidance by starlings under differing scenarios of predation risk. – Behav. Ecol. 17: 303–309.
- Elgar, M. A. 1989. Predator vigilance and group size in mammals and birds: a critical review of the empirical evidence. – Biol. Rev. 64: 13–33.
- Elgar, M. A. and Catterall, C. P. 1981. Flocking and predator surveillance in house sparrows: test of an hypothesis. – Anim. Behav. 29: 868–872.
- Fairbanks, B. and Dobson, F. S. 2007. Mechanisms of the group-size effect on vigilance in Columbian ground squirrels: dilution versus detection. – Anim. Behav. 73: 115–123.
- Fernandez-Juricic, E. and Kacelnik, A. 2004. Information transfer and gain in flocks: the effects of quality and quantity of social information at different neighbour distances. – Behav. Ecol. Sociobiol. 55: 502–511.
- Fernandez-Juricic, E. et al. 2004. Flock density, social foraging, and scanning: an experiment with starlings. – Behav. Ecol. 15: 371–379.
- Fernandez-Juricic, E. et al. 2005. Increasing the costs of conspecific scanning in socially foraging starlings affects vigilance and foraging behaviour. – Anim. Behav. 69: 73–81.
- Festa-Bianchet, M. et al. 2006. Stochastic predation events and population persistence in bighorn sheep. – Proc. R. Soc. B. 273: 1537–1543.
- Frid, A. 1997. Vigilance by female Dall's sheep: interaction between predation risk factors. – Anim. Behav. 53: 799–808.
- Giraldeau, L.-A. and Caraco, T. 2000. Social foraging theory. – Princeton Univ. Press.
- Gross, M. R. 1996. Alternative reproductive strategies and tactics: diversity within sexes. – Trends Ecol. Evol. 11: 92–98.
- Hamilton, W. D. 1971. Geometry of the selfish herd. – J. Theor. Biol. 31: 295–311.
- Hass, C. C. 1989. Bighorn lamb mortality: predation, inbreeding, and population effects. – Can. J. Zool. 67: 699–705.
- Hogg, J. T. and Forbes, S. H. 1997. Mating in bighorn sheep: frequent male reproduction via a high-risk “unconventional” tactic. – Behav. Ecol. Sociobiol. 41: 33–48.
- Hurvich, C. M. and Tsai, C. L. 1989. Regression and time-series model selection in small sample sizes. – Biometrika 76: 297–307.
- Jarnemo, A. and Liberg, O. 2005. Red fox removal and roe deer fawn survival—a 14-year study. – J. Wildlife Manage. 69: 1090–1098.
- Jorgenson, J. T. et al. 1997. Effects of age, sex, disease, and density on survival of bighorn sheep. – Ecology 78: 1019–1032.
- Krebs, J. R. and Davies, N. B. 1993. An introduction to behavioural ecology. – Blackwell.
- Lima, S. L. 1990. The influence of models on the interpretation of vigilance. – In: Bekoff, M. and Jamieson, D. (eds), Interpretation and explanation in the study of animal behavior: Vol. 2. Explanation, evolution and adaptation. Westview Press, pp. 246–267.
- Lima, S. L. 1995. Back to the basics of anti-predatory vigilance: the group-size effect. – Anim. Behav. 49: 11–20.
- Lima, S. L. 1998. Nonlethal effects in the ecology of predator-prey interactions. – BioScience 48: 25–34.
- Lima, S. L. and Dill, L. M. 1990. Behavioral decisions made under the risk of predation: a review and prospectus. – Can. J. Zool. 68: 619–640.
- Lima, S. L. et al. 1999. Predation, scramble competition, and the vigilance group size effect in dark-eyed juncos (*Junco hyemalis*). – Behav. Ecol. Sociobiol. 46: 110–116.
- Lipetz, V. E. and Bekoff, M. 1982. Group size and vigilance in pronghorns. – Z. Tierpsychol. 58: 203–216.
- Lung, M. A. and 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.
- McNamara, J. M. and Houston, A. I. 1982. Short-term behaviour and life-time fitness. – In: McFarland, D. J. (ed.), Functional ontogeny. Pitman, pp. 60–87.
- McNamara, J. M. and Houston, A. I. 1992. Evolutionarily stable levels of vigilance as a function of group size. – Anim. Behav. 43: 641–658.
- Metcalf, N. B. 1984. The effects of mixed-species flocking on the vigilance of shorebirds: who do they trust? – Anim. Behav. 32: 986–993.
- Parker, G. A. 1984. The producer/scrounger model and its relevance to sexuality. – In: Barnard, C. J. (ed.), Producers and scroungers: strategies of exploitation and parasitism. Chapman and Hall, pp. 127–153.
- Pulliam, H. R. 1973. On the advantages of flocking. – J. Theor. Biol. 38: 419–429.
- Pulliam, H. R. et al. 1982. The scanning behaviour of Juncos: a game-theoretical approach. – J. Theor. Biol. 95: 89–103.
- Réale, D. and Festa-Bianchet, M. 2003. Predator-induced natural selection on temperament in bighorn ewes. – Anim. Behav. 65: 463–470.
- Roberts, G. 1996. Why individual vigilance declines as group size increases. – Anim. Behav. 51: 1077–1086.
- Ross, P. I. et al. 1997. Cougar predation on bighorn sheep in southwestern Alberta during winter. – Can. J. Zool. 75: 771–775.
- Ruckstuhl, K. E. and Festa-Bianchet, M. 2001. Group choice by subadult bighorn rams: trade-offs between foraging efficiency and predator avoidance. – Ethology 107: 161–172.
- Ruckstuhl, K. E. et al. 2003. Bite rates in Rocky Mountain bighorn sheep (*Ovis canadensis*): effects of season, age, sex and reproductive status. – Behav. Ecol. Sociobiol. 54: 167–173.
- Shrader, A. M. et al. 2007. Social information, social feeding, and competition in group-living goats (*Capra hircus*). – Behav. Ecol. 18: 103–107.
- Valone, T. J. 1989. Group foraging, public information, and patch estimation. – Oikos 56: 357–363.
- Williams, G. C. 1964. Measurement of consociation among fishes and comments on the evolution of schooling. – Publications, Mus. Biol., Michigan State Univ. 2: 349–384.