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Review

What is the magnitude of the group-size effect on vigilance?

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Vigilance has been predicted to decrease with group size due to increased predator detection and dilution of predation risk in larger groups. Although earlier literature reviews have provided ample support for this prediction, an increasing number of studies have failed to document a decline in vigilance with group size. In addition, support for this prediction has been based thus far on the *P* value of the relationship between vigilance and group size rather than on a quantitative assessment of effect magnitude. Here, I use a meta-analysis of empirical relationships between vigilance and group size in birds published in the last 35 years to provide a reassessment of the group-size effect on vigilance. Nearly one-third of all published relationships between vigilance and group size were not significant ($n = 172$). Results from the meta-analysis indicate weak to moderate negative correlations between group size and time spent vigilant ($n = 43$), scan frequency ($n = 29$), or scan duration ($n = 20$). The magnitude of the relationship was stronger in studies that controlled the amount of food available to birds. A funnel plot of the relationship between correlation coefficients and sample size failed to reveal an obvious publication bias. Although the meta-analysis results generally support the prediction that vigilance should decline with group size, a large amount of variation in vigilance remains unexplained in avian studies. *Key words:* birds, group size, meta-analysis, vigilance. *[Behav Ecol 19:1361–1368 (2008)]*

Animals often interrupt feeding bouts to scan their surroundings. Scanning is referred to as vigilance and may serve several purposes including detection of predation threats and assessment of within-group competition (Krause and Ruxton 2002). The study of animal vigilance has produced a wealth of theoretical and empirical work during the last 35 years (see Caro 2005 for a recent review). In particular, it has been recognized that animals in groups can reduce individual investment in vigilance against predators at no increased risk to themselves. The group-size effect on vigilance asserts that vigilance is expected to decrease with group size for 2 main reasons. First, the presence of more eyes and ears in a group allows an increase in predator detection (Pulliam 1973). Second, the presence of many bodies in a group allows a reduction in individual predation risk by simple dilution assuming that predators target a single individual during each attack and attack groups irrespective of size (Foster and Treherne 1981). Because the burden of detection and of predation can be shared among the many foragers in the group, models predict that individuals should reduce vigilance levels in groups and thus allocate more time to other fitness-enhancing activities such as foraging (Pulliam et al. 1982; McNamara and Houston 1992; Ale and Brown 2007).

Several literature reviews in birds and mammals have documented a group-size effect on vigilance providing overwhelming support for theoretical predictions (Elgar 1989; Lima and Dill 1990; Quenette 1990; Caro 2005). Nevertheless, 2 issues have been problematic when assessing the strength of the group-size effect on vigilance. First, the decline in vigilance with group size has failed to be documented in several species especially since the major critical review of vigilance by Elgar (1989) has been published (see, for instance, Treves 2000; Robinette and Ha 2001; Barbosa 2002). Support for the prediction should thus be reassessed in the light of these newer findings. Second, and more importantly, support for the group-size effect has only been evaluated thus far using the *P* value of the relationship between vigilance and group size. Whether a relationship between 2 variables is significant or not tells us little about the magnitude of the effect and how much variance is explained by the independent variable. It is well known that a significant relationship may nevertheless be a weak effect if sample size is very large. To determine the success of the prediction that relates vigilance to group size, it would be worthwhile moving from a qualitative assessment based on significance level to a more quantitative analysis based on standardized estimates of the magnitude of the group-size effect. Along these lines, Blumstein provided some estimates of the percentage of variance in vigilance explained by group size in some rodent species and found that group size explained relatively little variance in vigilance (Blumstein 1996). A survey across a broader taxonomic group would be needed to provide a fairer assessment of the magnitude of the group-size effect.

Here, I use a meta-analysis to document the magnitude of the group-size effect using studies that have been published since the early 70s. Meta-analysis provides standardized effect size statistics that are comparable across published results (Lipsey and Wilson 2001). Heterogeneity among published results in the magnitude of the group-size effect can also be examined and related to ecological factors to uncover potential factors that influence magnitude. I restricted the survey to

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avian studies given the large number of papers on the topic. Birds are especially suited for this type of analysis. Group foraging is widespread in birds (Beauchamp 2002). Given that the very first models of animal vigilance focused on birds, vigilance has also been examined in many bird species afterward. Because no fundamental differences in vigilance have been proposed from one taxonomic group to another (Caro 2005), the results of the meta-analysis should provide a general account of vigilance in animals.

I examined the magnitude of the group-size effect on 3 components of vigilance, namely, the proportion of time spent vigilant, the frequency of scanning, and the duration of scans. If group size is indeed a significant factor in animal vigilance, the correlation between group size and vigilance components that will emerge from the meta-analysis should be large, negative, and with narrow confidence limits.

METHODS

Data collection

I used a 2-pronged approach to conduct a large-scale survey of the literature on vigilance in birds. First, I relied on the references cited in earlier surveys of the literature on vigilance (Barnard and Thompson 1985; Elgar 1989; Lima and Dill 1990; Beauchamp 1998; Caro 2005). In addition, I performed searches using online databases using the following key words: vigilance, group size, flock size, birds, time budget, and antipredator.

My main focus was on vigilance in avian foraging aggregations. With 2 exceptions (Heinsohn 1987; Griesser 2003), studies dealt with temporary feeding aggregations with fluid group membership. In the above 2 exceptions, the same group members were probably present in several aggregations, but because group size still varied considerably from aggregation to aggregation the group-size effect on vigilance should still be expected. I excluded from the survey papers dealing with vigilance in nonforaging contexts such as resting, sleeping, or preening. Papers that only provided measures of vigilance at the group level (i.e., percentage of vigilant foragers in a group at a given time) were also excluded given that I focused only on changes in individual vigilance with group size. Papers that reported only changes in interscan intervals with group size were also excluded unless it was obvious that feeding was the only alternative to vigilance in which case interscan intervals were taken as a measure of vigilance frequency.

For the included papers, I gleaned additional information including whether or not the relationship between group size and vigilance was significant at the 0.05 alpha level, the sample size n, the maximum group size included in the analysis, the proportion of time spent vigilant by solitary foragers, whether the amount of food available to the birds was controlled by the researchers, and whether factors other than group size, such as temperature or sex, were included in the statistical analysis. Food availability was deemed controlled when researchers manipulated the amount of food experimentally or provided food in quantities too large to be depleted during the observation period or took variation in food density into account in their statistical analysis. Several papers documented the relationship between vigilance and group size for different subgroups, such as males or females, or under different conditions, such as high or low predation risk. The context under which any relationship between vigilance and group size was documented was also noted. Finally, body mass for each species was obtained from a recent handbook (Dunning 2008).

Meta-analysis

I carried out the meta-analysis of the group-size effect using a subset of the papers involving at least 3 distinct group sizes and providing a measurement of the group-size effect that could be translated into the coefficient of correlation r, the effect-size statistic that was used here. Many papers provided a correlation coefficient between vigilance and group size in the form of Pearson's or Spearman's r. In papers that involved several independent variables, I used the adjusted coefficient of determination provided in the paper or that I calculated from the data to obtain r. In these cases, the coefficient of determination associated with the effect of group size is adjusted for the number of independent variables in the model and represents a nonbiased estimator of effect size (Nakagawa and Cuthill 2007).

R values from each paper represented the unit of analysis. For papers that provided several r values, I selected only one value for the meta-analysis to reduce pseudoreplication using the following criteria. For papers that documented r values for each sex, I selected the values for males. For papers that documented r values for peripheral and central individuals in a group, I selected the values for peripheral individuals. For papers that documented r values at different levels of predation risk, I selected the values at the higher level of risk. These choices were made to reduce variability among papers. The effect of each of these ecological factors was nevertheless examined fully in a further analysis (see below).

Some species in the dataset are more studied than others and thus occurred in more than one paper. As a first step in the quantitative analysis of the magnitude of group-size effect, I treated r values from the same species as independent from each other. To examine the validity of this assumption, I ran a mixed linear model, with genus as a random factor, to examine the contribution of genus to the variance in r values for percentage time spent vigilant, vigilance frequency, and vigilance duration. I used the dataset including only one r value per study given that repeats within a study are not random replicates (for instance one study will report data for males and females separately or for different distances to cover). For all 3 variables, the contribution of genus to the variance of r values proved to be less than 1% indicating that very little variance is accounted for by genus alone. I conclude that it is acceptable to treat each study of the same species as independent replicates. However, future studies that aim to examine the evolution of r values as a function of ecological traits may wish to take phylogenetic relationships into account more formally (Adams 2008).

Statistical analysis

R values were converted to Z values using Fisher's transformation (Sokal and Rohlf 1995). Such Z values follow the normal distribution. Confidence intervals for Z values were obtained using standard equations (Nakagawa and Cuthill 2007) and back-transformed to r values when needed. This back-transformation leads to asymmetrical confidence intervals.

The first step in the statistical analysis is to weigh Z values obtained from each suitable relationship between vigilance and group size. Traditionally, in a meta-analysis, the weight is inversely proportional to the variance of the effect-size statistic, which in the case of Z is equivalent to weighing each study by $n - 3$ (Lipsey and Wilson 2001). With such a weighing system, relationships based on a larger sample size contribute more to the overall assessment of the group-size effect on vigilance. I used a fixed-effect model, with restricted maximum likelihood estimation and including only the intercept, to obtain the mean and standard error of the weighted estimates of Z. To assess heterogeneity of Z values among studies, I used the weighted residual sum-of-squares of the fixed-effect model including only the intercept, which can be tested against the chi-square distribution with $k - 1$ degrees of freedom (df). In this analysis, k represents the number of studies included (Lipsey and Wilson 2001). When the heterogeneity proved significant at the 0.10 significance level, a more liberal level given the low power of this test, I tested the effect of moderator variables, namely variables that can influence Z values among relationships such as body mass or sample size, using each moderator variable separately in the above fixed-effect model.

Assessment of publication bias

I used a funnel plot of r values against the sample size for each paper. In funnel plots, publication bias can be presumed to occur when large values of r only occur for studies with large sample sizes.

RESULTS

A total of 172 relationships between vigilance and group size were obtained using the inclusion criteria (Appendix, Supplementary Material). Several papers included many relationships between vigilance and group size. When only one relationship was selected from each paper as detailed above, the total number of papers was 120. In the first survey of the literature on vigilance in birds, Elgar (1989) examined 41 relationships gleaned from 36 distinct papers. The number of published relationships between vigilance and group size has nearly quadrupled since the last major survey. The plot of the number of papers examining the relationship between vigilance and group size as a function of published decade indicates no signs of abating (Figure 1).

More than one-third of the published relationships were not significant or significant but in the opposite direction to that predicted by vigilance models (Table 1). This is particularly true for scan duration, but negative results were also common for time spent vigilant and scan frequency. Prior to 1990, 19% of the relationships between time spent vigilant and group size were not significant or significant but in the opposite direction to those predicted by vigilance models (9 out of 47, Appendix), whereas this was true for 32% of the relationships (26 out of 81) after 1990, a 68% increase.

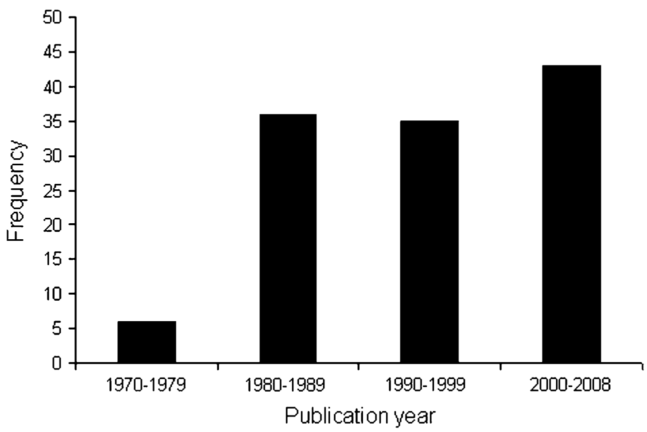

Figure 1
Evolution through the last 3 decades of the number of papers examining the effect of group size on vigilance in birds.

Table 1
Breakdown of the number of relationships between a component of vigilance and group size that were found to be significant and in the direction predicted that were found to be nonsignificant and finally significant but in the direction opposite to that predicted

Component	Predicted trend	No trend	Opposite trend	Total
Time spent vigilant	93 (72.7%)	33 (25.8%)	2 (1.5%)	128
Scan frequency	51 (64.6%)	23 (29.1%)	5 (6.3%)	79
Scan duration	18 (40.9%)	24 (54.5%)	2 (4.6%)	44

Meta-analysis

For time spent vigilant, the mean value of r was −0.42 (95% CI: −0.53, −0.29; $n = 43$; Figure 2), which is deemed a moderate effect using Cohen's terminology (Cohen 1988). The test for heterogeneity among Z values proved to be significant ($Q = 53.3$, $0.1 > P > 0.05$, df = 42) indicating that some moderator variables may be implicated. There was no significant relationship between the weighted values of Z and sample size (β = −0.19, 95% CI: −0.48, 0.11, $P = 0.21$), body mass (β = 0.000006; 95% CI: −0.000007, 0.000007; $P = 0.88$), maximum group size (β = −0.025; 95% CI: −0.19, 0.14; $P = 0.76$), or percentage time spent vigilant by solitary foragers (β = 0.0048; 95% CI: −0.0061, 0.016; $P = 0.39$). Z values did not differ significantly whether the statistical model of the relationship between vigilance and group size included only group size (mean = −0.51; 95% CI: −0.74, −0.28; $n = 25$) or group size and additional independent variables (mean = −0.34; 95% CI: −0.44, −0.24; $n = 18$; $P = 0.18$). However, Z values were significantly larger when food availability was controlled (mean = −0.64; 95% CI:

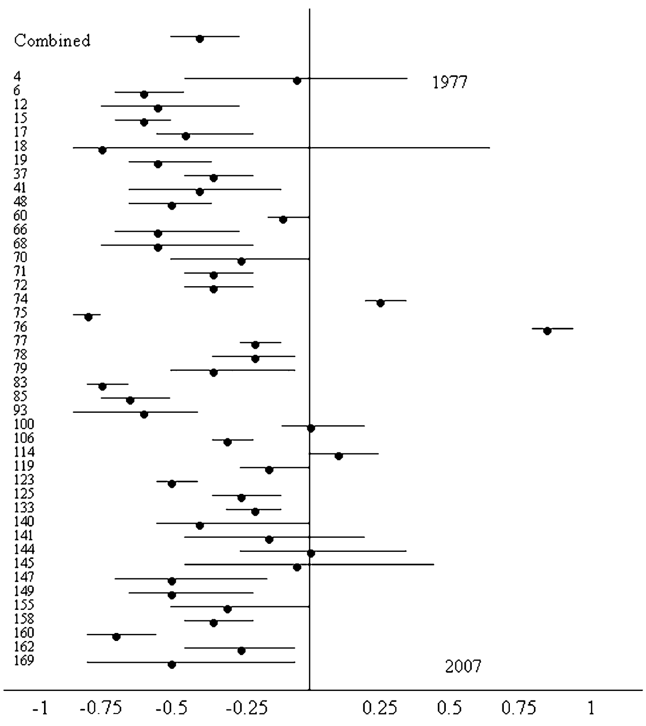

Figure 2
Confidence intervals of the coefficients of correlation between group size and percentage time spent vigilant ($n = 43$) in avian studies. Shown are the 95% confidence intervals around r values gleaned from each paper. The number associated with each study is shown on the left, and the range in publication years is shown on the right.

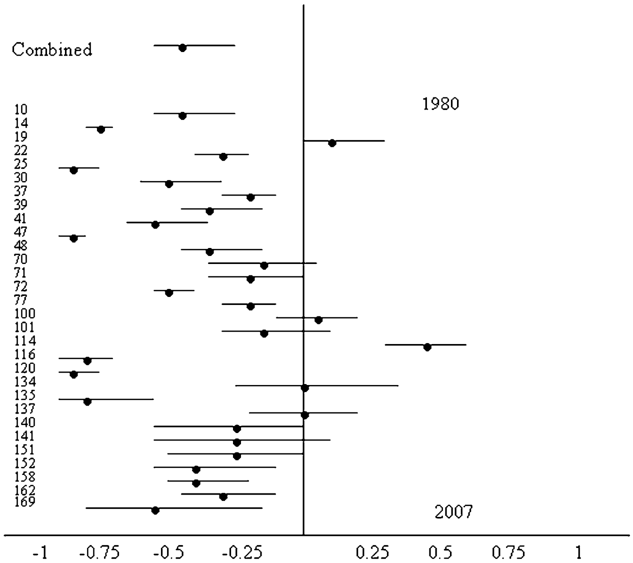

Figure 3
Confidence intervals of the coefficients of correlation between group size and scan frequency ($n = 29$) in avian studies. Shown are the 95% confidence intervals around r values gleaned from each paper. The number associated with each study is shown on the left, and the range in publication years is shown on the right.

-0.88, -0.40; $n = 11$) rather than not (mean $= -0.32$; 95% CI: -0.48, -0.16; $n = 35$; $P = 0.03$).

For scan frequency, the mean value of r was -0.47 (95% CI: -0.58, -0.28; $n = 29$; Figure 3), which is deemed a moderate effect. The test for heterogeneity of Z values among studies proved to be nonsignificant ($Q = 36.7$, $P > 0.1$, df $= 28$).

For scan duration, the mean value of r was -0.22 (95% CI: -0.32, -0.13; $n = 20$; Figure 4), which is deemed a weak effect. The test for heterogeneity of Z values among studies proved to be nonsignificant ($Q = 8.4$, $P > 0.9$, df $= 19$).

Publication bias

The funnel plot for the subset of papers reporting data on time spent vigilant failed to indicate the presence of an obvious publication bias. Indeed, the range of r values was similar whether sample size was small or large (Figure 5).

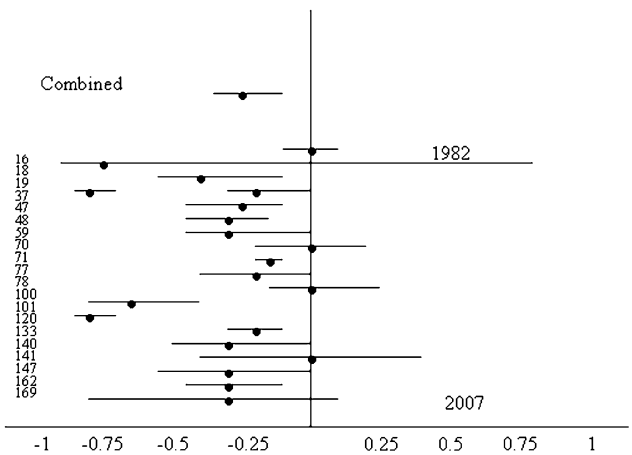

Figure 4
Confidence intervals of the coefficients of correlation between group size and scan duration ($n = 20$) in avian studies. Shown are the 95% confidence intervals around r values gleaned from each paper. The number associated with each study is shown on the left, and the scope in publication years is shown on the right.

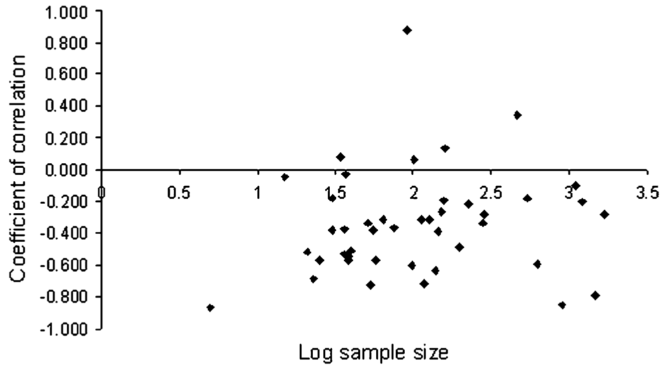

Figure 5
A funnel plot showing the relationship between r values and log sample size. R values represent the coefficient of correlation between group size and time spent vigilant obtained from 43 avian studies.

Sources of variation in the magnitude of the group-size effect within studies

The group-size effect was examined across levels of several ecological variables in many papers providing an opportunity to document sources of variation in the magnitude of the group-size effect within studies. There were too few studies to allow a test of r values between different levels of ecological variables. Instead, I used the level of significance of the relationship between group size and a component of vigilance as a simple criterion to assess the direction of the group-size effect. The following results are therefore not part of the meta-analysis and are presented in review style.

Effect of sex

Sexual differences in the strength of the group-size effect on time spent vigilant were examined in 7 species. One paper documented a significant effect of group size in females but not in males (Smith 1977), whereas another study documented the opposite effect (Reboreda and Fernandez 1997). In the remaining species, there was no sexual difference in the magnitude of the group-size effect (Hamed and Evans 1984; Beveridge and Deag 1987; Burger and Gochfeld 1988; Briggs 1990). Scan frequency decreased with group size to a greater extent in males than in females in 2 species (Beveridge and Deag 1987; Waite 1987b). The magnitude of the group-size effect on scan duration was larger in females than in males in house sparrows (*Passer domesticus*) but the same in chaffinches (*Fringilla coelebs*) (Beveridge and Deag 1987).

Spatial position in the group

With respect to spatial position in the group, the magnitude of the group-size effect was larger at the edge than at the center in European starlings (*Sturnus vulgaris*) (Keys and Dugatkin 1990), but the opposite was true in another study of the same species (Jennings and Evans 1980).

Predation risk

Predation risk has been manipulated in some studies usually by changing distance to cover and also by introducing a predator. In observational studies, predation risk was judged to differ between different study areas depending on habitat features such as vegetation height. A larger decrease in time spent vigilant with group size occurred under high risk than low risk in 3 species (Barnard 1980; Lendrem 1984; Lima 1987), whereas vigilance decreased to a larger extent at low risk than high risk in 2 other species (Martella et al. 1995; Lima et al. 1999). Time spent vigilant decreased with group size to the same extent both day and night in one species where night foraging was deemed to be riskier (Beauchamp and McNeil 2003). However, in the same species, scan duration decreased with group size at night but not during the day. Scan duration decreased to a similar extent under high and low predation risk in another species (Elgar 1986).

Visual obstacles

Presence of visual obstacles was manipulated by adding small walls between foraging birds, which presumably decreased the effectiveness of collective detection of predation threats. Time spent vigilant decreased to a larger extent with group size in the absence of visual obstacles in 2 species (Lima 1987; Lima and Zollner 1996). In another species, scan frequency tended to decrease more extensively with group size without visual obstruction (Harkin et al. 2000).

Dominance, feeder shape, type and dispersion of food, food deprivation, and kinship

The group-size effect on time spent vigilant was more pronounced in dominant birds than in subordinate birds in one species (Waite 1987a). In another species, scan frequency actually increased with group size in subordinate birds but not in dominant birds (Pravosudov and Grubb 1999). If adult birds are considered more dominant than juveniles, time spent vigilant decreased again to a larger extent with group size in the more dominant birds (Aviles and Bednekoff 2007). However, in this case, differences in foraging efficiency with age may confound the results.

Shape of the feeder where food is distributed played a role in some species. Time spent vigilant decreased to a larger extent in circular or square feeders than in narrow feeders (Bekoff 1995; Sadedin and Elgar 1998).

Type and dispersion of food can also alter the magnitude of the group-size effect. The decrease in scan duration with group size was more pronounced with a type of seeds that was handled during vigilance bouts than with a type that was handled during nonvigilant bouts (Lima et al. 1999). This effect however was only present in the low predation risk condition. Scan duration also decreased to a larger extent with group size when individuals fed on dispersed seeds than on clumped seeds (Cézilly and Brun 1989). Whether seeds are cryptic or not on the background did not influence the magnitude of the group-size effect on scan frequency and duration in one species (Courant and Giraldeau 2008).

Time spent vigilant decreased to a greater extent with group size in non–food-deprived birds than in food-deprived birds (Lima 1995). Finally, scan frequency decreased with group size to a greater extent in one species feeding with nonkin rather than with kin (Griesser 2003).

DISCUSSION

Relationships between components of vigilance in birds and group size have been published in large numbers and at a consistent rate over the last 3 decades providing an opportunity to examine in a quantitative fashion the magnitude of the group-size effect in a well-studied taxonomic group.

Qualitative assessment of the group-size effect in birds

The number of significant relationships between vigilance and group size is certainly high and in the direction predicted by theoretical models. However, nearly a third of all relationships were not significant or significant but in the opposite direction to that predicted by vigilance models. This was especially true for scan duration that proved the least correlated with group size in the meta-analysis. Given the wide confidence intervals that I documented in many studies, the nonsignificant results are probably due in part to low statistical power.

The lack of a significant relationship between vigilance and group size may also go beyond methodological issues. One possibility is that in many avian species vigilance can occur simultaneously with feeding reducing the need to adjust vigilance in large groups (Barbosa 2002). However, vigilance during food handling has been shown to decrease with group size in several avian species (Popp 1988; Beauchamp and Livoreil 1997; Lima et al. 1999) suggesting that adjustments in vigilance can also occur during food handling. Another hypothesis is that because vigilance can be aimed at other group members either to avoid aggressive displacement or to join their food discoveries, the expected decrease in vigilance with group size predicted from a predation risk point of view may be mitigated against by rival sources of attention (Treves 2000; Beauchamp 2001). Although increased aggression and/or scrounging opportunities can certainly be invoked in species where vigilance actually increases with group size as documented in several papers (e.g., Barnard and Thompson 1985; Knight and Knight 1986; Ely 1992; Bekoff et al. 1998; Goss-Custard et al. 1999; Pravosudov and Grubb 1999; Robinette and Ha 2001; Barbosa 2002), it is not clear to what extent these mechanisms can be implicated in studies documenting no effect of group size on vigilance. The lack of a relationship between vigilance and group size has also been noted frequently in mammals (e.g., Treves 2000; Laundré et al. 2001; Blumstein and Daniel 2002; Cameron and Du Toit 2005) indicating that avian and mammalian results are not qualitatively different and that the lack of a relationship is not specific to some taxonomic group. Future work could try to solve the puzzle as to why vigilance does not always decline with group size by looking at ecological attributes that are more prevalent in species where vigilance fails to decline with group size.

Meta-analysis

All 3 components of vigilance, namely, time spent vigilant, scan frequency, and scan duration, decreased significantly with group size in the meta-analysis of the subset of papers that provided effect size estimates. The correlation with group size was the strongest for time spent vigilant and scan frequency and the weakest for scan duration suggesting that overall adjustments in time spent vigilant are probably mostly related to scan frequency. Nevertheless, several studies reported significant decreases in scan duration with group size. In earlier vigilance models, scan duration was assumed to be very short and fixed in duration (Pulliam 1973; Pulliam et al. 1982; McNamara and Houston 1992). Results from the meta-analysis certainly suggest that this is an oversimplification in many avian species.

The magnitude of the group-size effect is considered moderate in size for time spent vigilant and scan frequency and weak for scan duration. Sample sizes in the 40–60 range should provide sufficient power to reject the null hypothesis at least for time spent vigilant and scan frequency. The overall significance of the group-size effect can be considered strong support for the theory underlying changes in vigilance with group size. How well does this overall support compare with results from other meta-analyses in behavioral ecology? The effect size for the relationship between fitness components and personality traits was found to be weak overall with absolute values of r around 0.1 (Smith and Blumstein 2008). The effect size for the relationship between bib size and age or fighting ability in house sparrows (*Passer domesticus*) was of similar magnitude to that uncovered for vigilance and group size with absolute *r* values ranging between 0.3 and 0.4 (Nakagawa et al. 2007). Similarly, the effect size for the relationship between escape distance and predator factors such as speed varied in absolute values between 0.3 and 0.7 (Stankowich and Blumstein 2005). In much of ecology and evolutionary biology, typical *r* values are of the order of 0.19 with most independent variables explaining less than 5% of the variation (Møller and Jennions 2002). Therefore, the effect of group size on vigilance is rather strong with respect to the overall picture in ecology.

Sources of variation in the magnitude of the group-size effect among studies

The magnitude of the group-size effect on time spent vigilant varied among studies but not for scan frequency and duration. Given that the heterogeneity test for *Z* values is not considered very powerful, it is possible that the smaller number of studies included in the meta-analysis of scan frequency and scan duration prevented the finding of a significant effect.

With respect to time spent vigilant, the magnitude of the group size was found to be similar in large and small species, in species that are more vigilant alone than others, in species found is small or large groups and in studies with a large or a small sample size. These results suggest that the magnitude of the group-size effect is similar across a wide range of species and is therefore a robust estimate. The implication is that although species may differ in the absolute amount of time spent vigilant at any given group size, the decrease in vigilance with group size is quite constant in magnitude.

The survey uncovered one important source of variation in the magnitude of the group-size effect among studies. Studies that controlled the amount of food provided to the birds, through food supplementation or actual measurement, reported a larger decrease in time spent vigilant with group size than uncontrolled studies. This is in contrast to a survey of papers on sexual selection in birds that documented similar effect sizes in experimental and observational studies (Gontard-Danek and Møller 1999). In their paper, the authors argued that this is unlikely to reflect the situation at large. Findings from the present meta-analysis support this conclusion. One possible reason for the effect of food control is that food was provided in large amounts in many of the controlled studies. With a large amount of food available, the level of food competition within the group may be decreased thus reducing the need to monitor companions. This reduction in the need to monitor companions is expected to reduce the investment in vigilance especially in the larger groups causing vigilance to decrease more extensively with group size.

It might be surprising at first sight that the magnitude of the group-size effect was not influenced by the use of statistical models including group size and additional independent variables rather than group size alone. Given that the extraneous variables, such as temperature (e.g., Beveridge and Deag 1987; Pravosudov and Grubb 1995), can also explain vigilance levels on their own, one would expect stronger *r* values in studies using multivariate regression analysis. However, as pointed out by Nakagawa and Cuthill (2007), a successful multivariate model may actually leave less variation to be explained by any independent variable. Comparisons of models with different number of independent variables and actually different independent variables may be therefore quite difficult.

As a final comment on factors that influence the magnitude of the group-size effect, it is important to realize that the definition of group size was not standardized across studies. Although it is clear where a group starts and ends in a dense but isolated aggregation, in many species individuals are scattered more widely and it is not immediately obvious at which distance the presence of group members effectively ceases to influence foraging behavior in companions. In one species, the magnitude of the group-size effect increased by excluding foragers that occurred beyond a certain distance (Blumstein et al. 2001). By effectively including only foragers that can influence each other, it might be possible to have a more standardized and operational definition of group size that could increase the statistical power of future studies on vigilance in animals.

Publication bias

Publication bias was assessed with a funnel plot and showed no obvious trends with respect to sample size. However, nonsignificant results or trends in the opposite direction to that predicted by vigilance models tended to be more common in more recent years with respect to time spent vigilant. This indicates at the very least that nonexpected results are being published. Publication bias is difficult to examine empirically given the lack of access to unpublished evidence. Nevertheless, in one concerted effort to assess publication bias, little evidence of bias was discovered in studies of sexual selection (Møller et al. 2005).

A more pernicious source of bias is whether effect size varies systematically between studies that report sufficient information to calculate effect size statistics and those where such statistics cannot be obtained (Cassey et al. 2004). In the present survey, an *r* value could only be obtained in about one-third of the cases, and it remains a possibility that the *r* values obtained are a biased estimator of the real values. In the subset of data with sufficient information to calculate *r* values for time spent vigilant, 16% of the relationships were not significant or significant but in the opposite direction to that predicted (7/43). In the subset of studies where *r* values could not be obtained but where *P* values were provided, this percentage was 36% (27 out of 76), a slightly but significantly higher percentage according to the chi-square test ($P = 0.04$). It is not clear how this bias affects the present findings. In contrast to the *r* values available thus far, unavailable *r* values may have the same magnitude but broader confidence intervals, in which case the overall value of *r* from the meta-analysis would remain the same but with broader confidence limits. Alternatively, unavailable *r* values could be closer to zero because they arise more often from nonsignificant relationships, in which case the overall value of *r* from the meta-analysis would be slightly overestimated. In any case, as pointed out by Cassey et al. (2002), to provide a fairer assessment of a biological relationship between any 2 variables, the information needed to calculate effect-size statistics should be provided regardless of the significance of the *P* values.

An increase in nonsignificant results over time, which has also been reported in other meta-analyses (Jennions and Møller 2002), may be a consequence of 2 factors. Since the late 1990s, several papers have argued that vigilance may not always decline with group size as a consequence of within-group competition or scrounging (Treves 2000; Beauchamp 2001; Barbosa 2002). Consequently, researchers may feel freer to publish nonsignificant results and discuss their results in the light of the above factors. The second reason is related to the fact that the magnitude of the group-size effect varies under different ecological conditions. The broader scope of vigilance studies in terms of species and environmental settings in recent years may mean that some studies are conducted under conditions where the magnitude of the group-size effect is expected to be low contributing to more negative results.

Sources of variation in the group-size effect within studies

Although the overall correlation between vigilance and group size is significant, group size explains generally less than 20% of the variation in vigilance. What could account for the wide scatter of data in any given relationship between vigilance and group size? The survey of variation in the magnitude of the group-size effect within studies points out a role for several ecological factors including sex, predation risk, spatial position within the group, presence of visual obstacles, type and distribution of food, kinship, and food deprivation level. The first implication of variation within studies in the magnitude of the group-size effect is that for any group size, scatter in the vigilance data will increase when individuals that are sampled from different groups of the same size vary with respect to any of the above variables. For instance, scatter in vigilance values will increase if individuals sampled from groups of the same size vary say with respect to hunger levels given that more hungry birds are less wary. The second implication is that it will be more difficult to document a group-size effect on vigilance when the magnitude of the effect is expected to be lower. It is certainly possible that many of the nonsignificant relationships between vigilance and group size uncovered in the survey may have been documented under conditions where the magnitude of the effect was not expected to be very strong in the first place. In future work, discussion of the ecological conditions under which the effect of group size on vigilance is examined seems warranted given the wide variation in effect size that can occur from one ecological context to another.

The effect of the above ecological factors on the magnitude of the group-size effect was often inconsistent from one species to another. This was the case especially for sex and predation risk. Such inconsistencies have also been noted in mammals with vigilance decreasing with group size to different extent in males or females but not always more extensively for the same sex from one species to another (Childress and Lung 2003; Cameron and Du Toit 2005; Shorrocks and Cokayne 2005). Similarly, vigilance decreases with group size to different extent when predation risk is high or low but not always more extensively at the same level of risk (Frid 1997; Hunter and Skinner 1998; Burger et al. 2000; Childress and Lung 2003; Manor and Saltz 2003). At the moment, no single model of vigilance can account for all these variations in the magnitude of the group-size effect on vigilance.

In conclusion, support for the prediction that vigilance should decline with group size is strong but a large amount of variation in the relationships remains unexplained. A challenge for future work will be to determine the ecological factors that underlie variation in the magnitude of the group-size effect on vigilance in birds and in other animals.

SUPPLEMENTARY MATERIAL

Supplementary material can be found at http://www.beheco.oxfordjournals.org/.

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