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Ontogenetic and Sex Differences Influence Alarm Call Responses in Mammals: a Meta-Analysis

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(Invited Review)

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Abstract

Animals respond to alarm calls by increasing their antipredator behavior; however, responses may consistently differ by age or sex. Although several adaptive explanations have been proposed to account for age-dependent antipredator behavior, similar explanations are rarely extended to sex-specific responses. Furthermore, no attempts have been made to quantitatively estimate the direction or magnitude of these differences across studies. Here, we use meta-analysis to discover overall trends in the literature, as well as differences owing to experimental or population parameters. Across our sample of available studies (unfortunately biased toward rodents and primates), males respond more than females, and young respond more than adults. Furthermore, young of quickly maturing species display more adult-like antipredator behavior than young of slowly maturing species, suggesting that young must develop antipredator behavior at a pace consistent with the length of their ontogenetic period (a.k.a. juvenile/sub-adult period, defined as the time between birth and attainment of sexual maturity). We review previously proposed explanations for such age differences, namely, that longer ontogenetic periods may provide juveniles with time to develop behavior through learning and experience, or, maturation rates may influence age-specific selection pressures and the consequent evolution of age-specific behavioral strategies. We evaluate our results in light of these hypotheses, although our conclusions are limited by the number and taxonomic bias of available studies. We therefore suggest ways in which future studies may tease apart the relative importance of learning and experience vs. age-specific adaptive behavior, and draw attention to opportunities for research on age- and sex-specific alarm call responses.

Introduction

Animals of many species alarm call to warn conspecifics of impending danger, and the response of adults to these vocalizations has been well studied (reviewed in Caro 2005). However, less attention has been paid to juvenile responses and the development of alarm calling behavior (reviewed in Hollen & Radford 2009). Young and adults differ in their reactions to alarm calls, and two major hypotheses have been proposed to explain this disparity (Hollen & Manser 2006; Hollen & Radford 2009). Under the first hypothesis, young require experience and physiological development to attain appropriate, adult-like responses, and differences between adults and juveniles are owing to errors that juveniles make while developing their antipredator behavior (Seyfarth & Cheney 1980; Hauser 1988). By contrast,

young may employ distinct antipredator strategies that reflect differences in selective pressures among age classes (Cheney & Seyfarth 1983; Owings & Loughry 1985; Hanson & Coss 2001). Under the latter hypothesis, age-specific strategies are viewed as adaptive, and ontogenetic variation among species may echo variation in factors influencing age-specific survival (e.g., maturation and growth rates, predator types, parental care, dispersal strategies).

For example, parental care affords young protection from predators as well as the opportunity to learn from a related demonstrator; such advantages are likely to decrease juvenile mortality and consequently reduce selective pressures on juvenile antipredator behavior (Hollen & Manser 2006). Furthermore, in species that reach sexual maturity or disperse immediately following their first year of life, we may expect young and adult individuals to display similar antipredator behavior owing to increased selective pressure. Individuals of such quickly maturing species are expected to cope independently with predation risks at a young age, and adult-like responses may be expected early in life.

Interestingly, sex differences in alarm call response have received minimal attention, although similar risk-dependent logic should apply. In many species, mortality rates vary between sexes (e.g., meerkats (*Suricata suricatta*) Russell et al. 2002; yellow-bellied marmots (*Marmota flaviventris*) Borrego et al. 2008), and we should expect males and females to differ accordingly in their antipredator behavior. However, such results are not consistently reported or tested for, and antipredator behavior is often assumed to be consistent between sexes.

The few studies that do compare alarm call responses among age or sex classes have reported mixed results across, and in some cases within, species. For example, Loughry & McDonough (1989) observed similar levels of vigilance in adult and juvenile California ground squirrels (*Spermophilus beecheyi*) following chatter alarm calls, while another study found that adults engaged in significantly more orienting behavior than juveniles following conspecific chatter (Hanson & Coss 2001). Although the hypotheses (discussed earlier) have been proposed as explanations for variation in age-specific behavioral strategies *among* species, the reporting of different ontogenetic trends *within* a species indicates that our view of age differences in antipredator behavior is still incomplete. The nature of selective pressures (e.g., predator types and predation levels) may differ between populations resulting in varied ontogenetic trends within a species. Furthermore, experimental details likely contribute to conflicting results.

Here, we gather all available studies reporting age and sex differences in mammalian alarm call responses. We performed a formal meta-analysis, in which we estimated the magnitude of age and sex differences in alarm call response across mammalian populations. Although meta-analyses have populated the psychological and medical literature for decades, this rigorous, systematic method for evaluating results across studies has been underappreciated by behavioral ecologists. In a meta-analysis, the results from all available studies on a particular topic are gathered and each is assigned an effect size (a standardized measure of response magnitude). To estimate the average response magnitude for a group of studies (e.g., do young animals respond more to alarm calls than adults?), a $\bar{x}$ effect size measures is calculated. Here, studies with larger sample sizes are given more weight to control for sample size differences across studies. Furthermore, studies may be partitioned into categories to examine the influence of biological or experimental variables on measures of effect size (Gurevitch et al. 2000). For example, do studies of captive vs. free-living animals report results of similar magnitude? In this manner, meta-analysis allows us to understand which factors explain variation in results across studies. In general, meta-analysis assures that results across studies are not only reviewed, but also quantified and compared at a more precise level than simply significant vs. non-significant (a.k.a. vote counting).

We wished to perform a formal meta-analysis, rather than simply a traditional review, to understand the magnitude of differences in antipredator between young vs. adults and males vs. females, as well as the biological and experimental variables that significantly explain variation between studies. We partitioned studies into subgroups to understand the influence of taxon, as well as experiment (measure type, stimulus) and population (free-living vs. captive study subjects, age at sexual maturity) features, on age differences in antipredator behavior. Furthermore, we used meta-analysis to test specific hypothesis. We predicted that slowly maturing species display less adult-like responses to alarm calls than young of quickly developing species. Although the influence of ontogeny on antipredator behavior is often discussed, this is the first attempt to synthesize studies on the topic and understand the magnitude of its effects across species. We conclude with a call for additional studies to improve the power of future meta-analyses and propose meaningful ways in

which researchers may expand upon this understudied topic.

Methods

Data Collection

To obtain data on age and sex differences in alarm call response, we first collected all studies cited in Table 1 of Hollen & Radford (2009). We then searched the Web of Science database (isiknowledge.com) using the following terms: age, sex, juvenile, alarm call, playback, response, vigilance, anti-predator, and foraging. 'Alarm call' was always included as a search term and was then combined with a subject term (age, sex, juvenile) and/or a study term (playback, response, vigilance, anti-predator, foraging). Subject terms and study terms were searched alone and in all combinations. This method yielded 363 results. We focused our analysis on mammalian responses to conspecific alarm calls, because this class included the largest number of comparable studies. Furthermore, we were interested in broad age differences in responsiveness and eliminated studies that focused on a single age class. We also eliminated studies that observed or anecdotally discussed age or sex differences but did not report statistical tests or descriptive statistics. In total, 17 studies (with publication dates ranging from 1980 to 2009) comparing adult vs. young and 9 (1989–2009) comparing male vs. female responses met our criteria (see Table 1). Our sample was therefore small; however, meta-analysis techniques are commonly used in other fields to synthesize results from an even more limited number of studies (e.g., McNamara et al. 2001: $N = 5$; Gatta et al. 2007: $N = 5$; Michalski et al. 2007: $N = 3$). Meta-analysis is a powerful and accepted tool for identifying patterns among studies, even when few attempts have been made to address the particular topic (Glass 1976; Rosenthal 1991); we therefore believed that a meta-analysis on this poorly addressed, although extremely important, behavioral issue would provide important insight and encourage future studies on the topic.

For each study, we noted the following information: year of publication, author(s), study species, population type (free-living or captive/provisioned), the measurement (time allocation, flee response, or response categorized into broad behaviors without quantitative measures of activity) used to quantify response, the origin of the stimulus (playback or natural), the age class of the caller (young or adult as defined by sexual maturity), sample size, test statistics and/or $\bar{x}$, and p values. We hypothesized that the above population and study features would explain variation in effect sizes, and subgroups were therefore created to examine effect size differences among these groups. These categories were analyzed for the age data set only, because so few studies were available for analyses of sex differences.

Calculating Effect Size

We converted reported statistics to Hedges' d (Hedges & Olkin 1985)-a standardized, unbiased measure of effect size (calculated as the difference between experimental and control group $\bar{x}$ divided by their pooled standard deviation and corrected for sample size). Hedges' d is appropriate for categorical predictor variables and small sample sizes (Nakagawa & Cuthill 2007) and is often used to assess biological studies (e.g., Møller & Jennions 2002). Hedges' d is not to be confused with Cohen's d (another common measure of effect size with a different equation for calculating pooled standard deviations) or Hedges' g; Hedges' g is equivalent to Hedges' d but lacks the correction for sample size that is included in Hedges' d (Hedges & Olkin 1985; see Data S1). Hedges' d was obtained for each study in the following ways (in order of preference): direct reporting of effect size, test statistics (e.g., F, t, χ^2) converted to d using methods in Rosenthal (1991) and Borenstein et al. (2009), and $\bar{x}$ and variance data (standard error or deviation) reported directly in the text or measured from figures and converted to d using equations in Hedges & Olkin (1985). Studies that reported simply $p > 0.05$ or stated that results were 'not significant' were included with a d score of 0 (i.e., $p = 0.5$). Some meta-analyses (e.g., Stankowich & Blumstein 2005) exclude studies with such incomplete reporting; however, we did not wish to bias our sample in favor of studies with positive results. All analyses were performed with and without non-significant (alpha = 0.05) studies, and where similar results were obtained, we report the inclusive results.

We arbitrarily assigned directionality to effect sizes (to test hypotheses) such that $d < 0$ was interpreted as young or females responding more than adults or males to alarm calls. We interpreted responsiveness as suggested by the authors of a particular study; in general, age and sex classes that suppressed foraging, increased their vigilance, or fled the area were classified as more responsive to alarm calls.

For studies reporting more than one experiment (i.e., stimulus), we treated each experiment as an independent study with a unique effect size

Table 1: Summary of data used in meta-analyses with each row corresponding to a unique experiment. PB refers to the results from playback experiments; *N* refers to natural observations of responses to calls. References for meta-analysis data as well as age (in years) at sexual maturity (i.e., age at which animals are able to successfully reproduce) are provided

Species	Experiment/stimulus	*N*	*d*	Population	Measure type	Age at sexual maturity	Reference(s)
Age (adult vs. young)							
Barbary macaqus (*Macaca sylvanus*)	Adult double call (PB)	59	−1.093	Captive	Categorize	>3	1, 22
Barbary macaque (*M. sylvanus*)	Adult single call (PB)	80	−0.792	Captive	Categorize	>3	1, 22
Belding's ground squirrel (*Spermophilus beldingi*)	Adult trill (PB)	99	−0.821	Free-living	Categorize	1	2, 23
Belding's ground squirrel (*S. beldingi*)	Adult whistle (PB)	48	−0.476	Free-living	Categorize	1	2, 23
Belding's ground squirrel (*S. beldingi*)	Adult whistle chorus (PB)	58	−0.275	Free-living	Categorize	1	2, 23
Belding's ground squirrel (*S. beldingi*)	Adult trill (PB)	81	0.000	Free-living	Time	1	3, 23
Belding's ground squirrel (*S. beldingi*)	Adult whistle (PB)	81	0.000	Free-living	Time	1	3, 23
Belding's ground squirrel (*S. beldingi*)	Adult whistle chorus, whistle, trill (PB)	72	−0.185/−0.536	Captive	Time/categorize	1	4, 23
Bonnet macaque (*Macaca radiata*)	Juvenile (PB)	44	−0.880	Free-living	Flee	>3	5, 29
Bonnet macaque (*M. radiata*)	Adult (PB)	59	0.000	Free-living	Flee	>3	5, 29
California ground squirrel (*Spermophilus beecheyi*)	Adult chatter (PB)	18	1.178/−1.451	Free-living	Time/flee	1	6, 24
California ground squirrel (*S. beecheyi*)	Adult whistle (PB)	20	0.287/0.596	Free-living	Time/flee	1	6, 24
California ground squirrel (*S. beecheyi*)	Non-repetitive (N)	21	0.382	Free-living	Time	1	7, 24
California ground squirrel (*S. beecheyi*)	Repetitive (N)	21	0.555	Free-living	Time	1	7, 24
California ground squirrel (*S. beecheyi*)	Chatter and repetitive (PB)	24	−0.581	Free-living	Categorize	1	8, 24
Meerkat (*Suricata suricatta*)	Adult call to aerial non-predator (N)	96	−0.978	Free-living	Categorize	1	9, 19
Meerkat (*S. suricatta*)	Adult call to aerial predator (N)	96	0.563	Free-living	Categorize	1	9, 19
Meerkat (*S. suricatta*)	Adult (PB)	58	1.550	Free-living	Time	1	9, 19
Richardson's ground squirrel (*Spermophilus richardsonii*)	One juvenile caller (PB)	53	−0.810	Free-living	Time	1	10, 25
Richardson's ground squirrel (*S. richardsonii*)	Two juvenile callers (PB)	53	−0.281	Free-living	Time	1	10, 25
Richardson's ground squirrel (*S. richardsonii*)	Adult repetitive (PB)	93	0.359/0.358	Free-living	Time/Categorize	1	11, 25
Richardson's ground squirrel (*S. richardsonii*))	Juvenile repetitive (PB)	93	0.010/−0.404	Free-living	Time/Categorize	1	11, 25
Ring-tailed lemur (*Lemur catta*)	Adult anticarnivore (PB)	32	0.000	Captive	Flee	1–3	12, 20
Ring-tailed lemur (*L. catta*)	Adult antiraptor (PB)	28	−0.802	Captive	Flee	1–3	12, 20
Ruffed lemur (*Varecia variegata*)	Adult anticarnivore (PB)	21	−1.689	Captive	Flee	1–3	12, 28
Ruffed lemur (*V. variegata*)	Adult antiraptor (PB)	16	−2.049	Captive	Flee	1–3	12, 28
Squirrel monkey *(Saimiri sciureus)*	Infant peep (PB)	17	−0.922	Captive	Flee	1–3	13, 21
Squirrel monkey *(S. sciureus)*	Juvenile peep (PB)	17	−0.817	Captive	Flee	1–3	13, 21
Squirrel monkey *(S. sciureus)*	Adult peep (PB)	17	−0.894	Captive	Flee	1–3	13, 21
Thirteen-lined ground squirrel (*Spermophilus tridecemlineatus*)	Adult trill (PB)	30	−0.599	Free-living	Flee	1	14, 26
Vervet monkey (*Cercopithecus aethiops*)	Leopard, eagle, snake (PB)	56	−0.230	Free-living	NA	>3	15, 27
Yellow-bellied marmot (*Marmota flaviventris*)	Adult (PB)	22	−0.240	Free-living	Time	1–3	16, 30
Yellow-bellied marmot (*M. flaviventris*)	Adult (PB)	45	−1.645	Free-living	Time	1–3	17, 30
Sex (male vs. female)							
Belding's ground squirrel (*S. beldingi*)	Adult trill (PB)	99	0.000				2
Belding's ground squirrel (*S. beldingi*)	Adult whistle (PB)	99	0.000				2
Belding's ground squirrel (*S. beldingi*)	Adult whistle chorus (PB)	99	0.000				2

Table 1: (Continued)

Species	Experiment/stimulus	*N*	*d*	Population	Measure type	Age at sexual maturity	Reference(s)
Belding's ground squirrel (*S. beldingi*)	Adult trill (PB)	81	0.000				3
Belding's ground squirrel (*S. beldingi*)	Adult whistle (PB)	81	0.000				3
California ground squirrel (*S. beecheyi*)	Juvenile chatter (PB)	9	0.000				6
California ground squirrel (*S. beecheyi*)	Juvenile whistle (PB)	9	0.000				6
California ground squirrel (*S. beecheyi*)	Non-repetitive chatter before pup emergence (N)	12	0.297				7
California ground squirrel (*S. beecheyi*)	Repetitive before pup emergence (N)	12	1.866				7
Great gerbil (*Rhombomys opimus*)	Rhythmic (PB)	18	0.000				18
Great gerbil (*R. opimus*)	Fast/intense (PB)	18	0.000				18
Great gerbil (*R. opimus*)	Whistle (PB)	18	0.000				18
Meerkat (*S. suricatta*)	Adult (N)	48	0.325				9
Meerkat (*S. suricatta*)	Adult (PB)	16	0.858				9
Squirrel monkey (*Saimiri sciureus*)	Infant and juvenile peep (PB)	17	0.000				13
Yellow-bellied marmot (*M. flaviventris*)	Adult (PB)	22	0.236				16
Yellow-bellied marmot (*M. flaviventris*)	Adult (PB)	45	1.125				17

1-Fischer et al. (1995), 2-Mateo (1996), 3-Mateo (2007), 4-Mateo & Holmes (1997), 5-Ramikrishnan & Coss (2000), 6-Hanson & Coss (2001), 7-Loughry & McDonough (1989), 8-Rabin et al. (2006), 9-Hollen & Manser (2006), 10-Sloan & Hare (2008), 11-Swan & Hare (2008), 12-Macedonia (1990), 13-McCowan et al. (2001), 14-Schwagmeyer & Brown (1981), 15-Seyfarth & Cheney (1980), 16-Blumstein & Récapet (2009), 17-Lea & Blumstein (2011), 18-Randall & Rogovin (2002), 19-Spong et al. (2008), 20-Sussman (1992), 21-Boinski (1987), 22-Kuester & Paul (1996), 23-Morton & Tung (1971), 24-Evans & Holdenried (1943), 25-Michener (1989), 26-Rongstad (1965), 27-Cheney & Seyfarth (1988), 28-Long (2003), 29-Rao et al. (1998), 30-Blumstein & Armitage (1999).

(following Stankowich & Blumstein 2005; Boonekamp et al. 2008). Many studies reported more than one result within an experiment, and in such cases only one response measure was included in each subgroup analysis. If more than one measure was available for a given subgroup, studies were selected in order of statistical preference (see earlier). For example, if an experiment demonstrated that alarm calls affected time allocated to vigilance ($\bar{x}$ proportion provided) as well as time allocated to foraging (effect size statistic provided), we included the foraging data in our analysis.

Meta-Analyses

All meta-analyses were performed in META-ANALYSIS Programs 5.3 (Ralf Schwarzer: http://web.fu-berlin.de/gesund/gesu_engl/meta_e.htm) using fixed and random effects models (Hedges & Olkin 1985; Borenstein et al. 2009). The fixed effects method is more popular, but not always appropriate (Fleiss 1993). Fixed effects models assume that study designs are similar and populations share a common effect size, while a random effects model assumes that effect sizes differ between studies as a result of experimental or population features. This approach seemed more appropriate for our data; however, we present results from both models to allow for comparison (Table 2).

For each subgroup, we tested the significance of results using the *Z* test (Rosenthal 1991). To examine heterogeneity, we calculated I^2—the percent of variation owing to true differences in study results (Higgins et al. 2003). Negative values of I^2 were set to 0%, representing little or no variation in *d* scores. For heterogeneous groups, we used cluster analysis to identify homogenous subgroups at the 5% significance level. When studies clustered by taxon or some feature of study design, we reran meta-analyses as described earlier.

Meta-analysis methods assume that the literature available for review is unbiased (Rosenthal 1991); however, this is rarely the case. It is more likely that some publication bias exists, typically with negative or non-significant results remaining unpublished. Several methods for estimating publication bias are available (reviewed in Møller & Jennions 2001), but the more popular approaches (i.e., fail safe numbers, rank correlation tests) require relatively large data sets and should be used with caution in small meta-analyses (Begg & Mazumdar 1994). Owing to the small number of studies in our data set, we used funnel plots to visualize potential

Table 2: Results from random and fixed effects meta-analyses with effect size (*d*), standard error of effect size (SE), *Z*-score, percent of variation owing to differences in study results (I^2), total number of studies (K_1), total number of experiments (K_2), and combined sample size (*N*) reported for each subgroup analysis. Combined sample size refers to the total number of individual responses compiled across studies

	Random effects model				Fixed effects model						
Subgroups	*d*	SE	*Z*	I^2 (%)	*d*	SE	*Z*	I^2	K_1	K_2	*N*
Adult vs. young											
All experiments	−0.328	0.129	−2.554**	78.952	−0.270	0.052	−5.092**	78.188	17	33	1669
Exclude p = 0.5	−0.365	0.140	−2.606**	80.593	−0.297	0.054	−5.345**	79.769	16	30	1475
Exclude ruffed lemur	−0.264	0.119	−2.216*	78.442	−0.246	0.052	−4.590**	77.391	16	31	1632
Ruffed lemur only	−1.746	0.417	−4.185**	0.000	−1.746	0.395	−4.411**	0.000	1	2	37
Measure type											
Time allocated to vigilance or foraging	0.051	0.203	0.249	82.736	−0.014	0.074	−0.177	80.545	9	14	797
Flee response	−0.675	0.200	−3.370**	54.510	−0.580	0.121	−4.679**	48.845	6	12	307
Exclude ruffed lemur	−0.498	0.176	−2.835**	41.804	−0.465	0.128	−3.554**	30.534	5	10	270
Categorize behavior	−0.432	0.152	−2.836**	80.759	−0.383	0.072	−5.258**	77.007	6	11	855
Subjects											
Captive/provisioned	−0.749	0.167	−4.485**	54.065	−0.617	0.104	−5.844**	46.426	6	10	405
Exclude ruffed lemur	−0.538	0.110	−4.896**	39.759	−0.538	0.109	−4.916**	23.104	5	8	368
Free-living	−0.145	0.146	−0.993	81.393	−0.154	0.060	−2.511	80.052	11	23	1264
Primates	−0.708	0.156	−4.530**	45.759	−0.656	0.103	−6.307**	38.560	5	12	430
Exclude ruffed lemur	−0.582	0.108	−5.381**	30.016	−0.582	0.107	−5.405**	14.950	4	10	393
Squirrels	−0.208	0.142	−1.461	69.567	−0.215	0.068	−3.100**	66.642	11	18	989
Exclude 2 outliers	−0.175	0.097	−1.816*	42.130	−0.162	0.072	−2.243*	34.755	10	16	908
Stimulus											
Natural	0.077	0.363	0.212	89.715	−0.060	0.131	0.445	82.959	2	4	234
Exclude call to non-predator	0.525	0.174	3.023*	0.000	0.525	0.173	3.030*	0.000	2	3	138
Playback	−0.386	0.135	−2.854**	76.671	−0.308	0.056	−5.349**	75.734	17	29	1435
Adult alarm call	−0.332	0.174	−1.913*	83.834	−0.262	0.060	−4.2514*	82.830	13	23	1270
Young alarm call	−0.409	0.126	−3.250**	44.444	−0.409	0.125	−3.260**	22.891	3	6	277
Exclude Richardson's ground squirrels	−0.848	0.257	−3.296**	0.000	−0.848	0.255	−3.328**	0.000	2	3	78
Richardson's ground squirrels only	−0.324	0.235	−1.378	61.240	−0.271	0.143	−1.878*	22.933	1	3	199
Sexual maturity											
Age 1	−0.032	0.150	−0.214	79.457	−0.067	0.062	−1.053	77.511	10	19	1156
1 < Age < 3	−0.923	0.209	−4.423**	56.726	−0.935	0.144	−6.335**	47.666	4	9	231
Exclude ruffed lemur	−0.768	0.221	−3.482**	64.286	−0.821	0.169	−4.755**	50.683	4	6	166
Age > 3	−0.592	0.203	−2.920**	57.128	−0.599	0.126	−4.730**	35.991	3	5	282
Male vs. female											
All experiments	0.164	0.083	1.976*	23.357	0.156	0.077	2.003*	18.089	9	17	695
Exclude p = 0.5	0.681	0.218	3.120**	31.973	0.684	0.160	4.226**	9.976	4	6	171

*p < 0.05, **p < 0.001.

publication bias (see Cassey et al. 2005; Nakagawa & Cuthill 2007).

Results

Publication Bias

Publication bias appears to be an issue for studies of sex (Fig. 1a) and to a lesser extent age (Fig. 1b) differences in responsiveness to alarm calls. In the absence of bias, a plot relating effect size to sample size should reveal a funnel, with larger variances corresponding to studies of decreasing sample size (Møller & Jennions 2001). Such a plot would converge on the true population effect size (i.e., the tip of the funnel). For our meta-analysis of sex differences in antipredator behavior, we observed a skew toward larger effect sizes when sample size was low (as expected owing to larger variation in reported effect size from small data sets). Publication of sex-related differences in alarm call response was biased toward males; no studies reported females more responsive to alarm calls than males (even among studies with small sample sizes).

For studies of age differences, variation in effect size decreases somewhat with increasing sample size, but there does not appear to be a consistent true effect size across studies. As sample sizes increase,

studies do not approach a 'true' effect size, and there is a large amount of heterogeneity in the data set (I^2 = 78.95%). Nevertheless, there does appear to be a slight publication bias among mid-sized studies, with more studies reporting juveniles as the most responsive age class (i.e., skew toward negative effect sizes).

Age and Sex Differences in Alarm Call Response

On average, males respond more to alarm calls than females and young respond more strongly than adults (Table 2, Fig. 2). Effect sizes for studies reporting age differences were heterogeneous across experiments, and removal of an outlier did not reduce heterogeneity.

When studies of age differences are partitioned into relevant categories, some variation is explained and interesting patterns emerge (Fig. 2, Table 2). For studies recording time allocation, adult and juvenile responses to alarm calls are similar. However, when researchers measured responsiveness by categorizing behavior or noting whether or not animals fled, young displayed more antipredator behavior than adults. Experiments incorporating played back calls report greater differences between age classes than studies of naturally occurring alarm calls, as do studies of calls from juvenile vs. adult conspecifics. However, only a handful of studies incorporated juvenile (N = 6) or naturally occurring (N = 4) calls and our discussion is therefore limited by our small data set. The captive vs. free-living subgroup comparison is also hindered by a lack of taxonomic diversity—nine of ten captive experiments involve primates. However, the $\bar{x}$ effect size of primate ($\bar{x}$ $d \pm$ SE = −0.708 ± 0.156) and captive ($\bar{x}$ $d \pm$ SE = −0.749 ± 0.167) studies is similar, suggesting that age-specific antipredator responses of captive populations are similar to those of primates generally.

We found sizeable differences between young and adult behavior in slow maturing species. Conversely, the antipredator response of juveniles of fast maturing species is typically indistinguishable from that of adults. Owing to a lack of biodiversity in our study, the quickly (Age 1 = 16 squirrel/19 total studies) and slowly (Age 1–3 yrs = seven primate/nine total studies, Age > 3 yrs = five primate/five total studies) maturing subgroups are composed of related species, and our results are confounded by taxa. When comparing primates vs. squirrels specifically, some heterogeneity was explained by taxa (with subgroups becoming substantially more homogenous when outliers were excluded). Following the results for maturation rate, we found more a trend for more pronounced age differences in primates than squirrels.

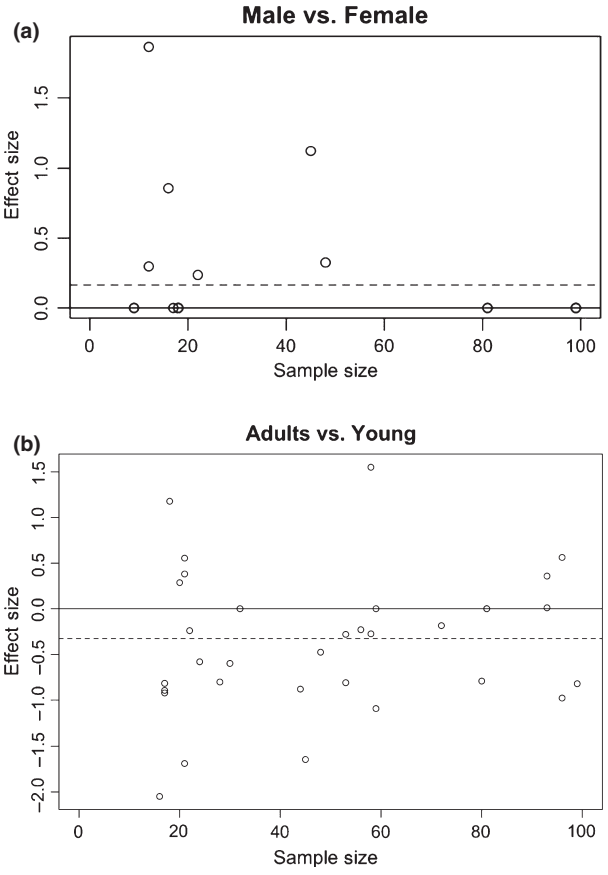

Fig. 1: (a) and (b). Funnel plots of studies used in meta-analyses of age and sex differences. Dashed lines represent the average effect size for each analysis (as determined by a random effects model); solid lines represent an effect size of zero.

Discussion

The results of our formal meta-analysis demonstrate that while both sex and age influence responsiveness to alarm calls, age is much more important than sex. This insight, which emphasizes the importance of development, was only possible because we formally estimated, and tested the significance of, $\bar{x}$ effect sizes. Furthermore, our methodology allowed us to identify and compare variables that significantly explain differences among studies. We discuss these results in detail later. An additional insight made possible from our formal meta-analysis is our detection of selective reporting in the literature. While this is not uncommon, it does justify future researchers reporting null or contradictory results.

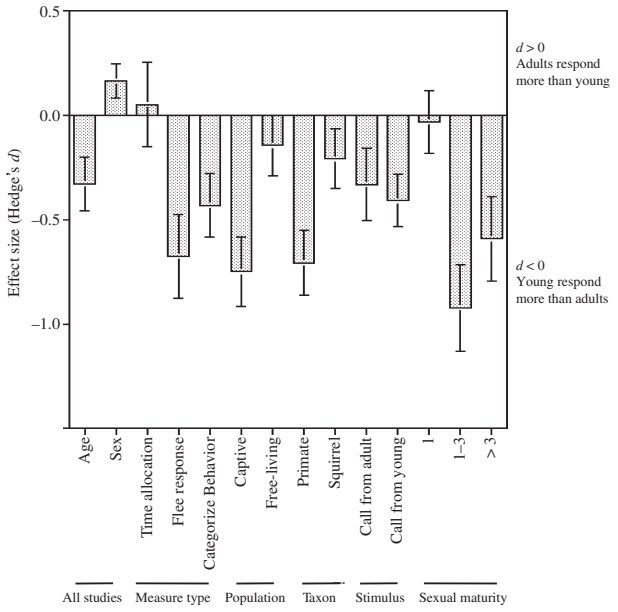

Fig. 2: Effect size measures ($\bar{x}$ $d \pm$ SE) for all analyses. The $\bar{x}$ effect size for studies comparing male and female responses ('sex' on the *y*-axis) is positive ($d > 0$), indicating that males respond more than females. All other analyses refer to differences between age classes.

Finally, our estimates of $\bar{x}$ effect size provide guidelines for sample sizes in future studies; because sex differences are less pronounced than age differences, larger sample sizes will be required to detect significant effects of sex on antipredator behavior. We discuss the results of our meta-analysis later, and end with guidelines future research on these topics.

Sex Differences in Alarm Call Response

Males and females consistently differ in their responses to conspecific alarm calls, with males typically responding more than females (although the average differences are small, Cohen 1988). Males may be more responsive to alarm calls than females as a result of their higher predation rates. Such differential survival is observed in several of the species included in our analysis (e.g., meerkats (*S. suricatta*) Russell et al. 2002; yellow-bellied marmots (*M. flaviventris*) Borrego et al. 2008) and may be related to sex-specific antipredator strategies. We encourage future research linking sex biases in responsiveness with sex-specific mortality and predation rates; pecifically, studies of species in which males and females experience similar mortality rates would be a useful addition to our discussion of the influence of sex-specific selection pressures on alarm call response.

Although the results of our meta-analysis suggest that increased predator-related mortality in males selects for increased responsiveness following alarm calls, alternative hypothesis should be examined. Females may experience higher nutritional demands than males (owing to the costs of reproduction or lactation), which may affect their willingness to suppress foraging or flee a feeding area. Food supplementation has been shown to decrease the magnitude of age-related differences in baseline vigilance levels (Arenz & Ledger 2000), and similar supplementation experiments may decrease the magnitude of sex-related differences in responsiveness as well; such experiments would provide valuable insight into factors controlling sex biases in alarm call response. Furthermore, mammalian males and females often differ in their response to stress (Kirschbaum et al. 1992; Tilbrook et al. 2000), and it is possible that differences in male and female neuroendocrine responses (Kudielka & Kirschbaum 2005) mediate responsiveness to alarm calls. Future research examining male and female neuroendocrine responses to alarm calls may uncover a proximate explanation for sex-related differences in antipredator behavior.

Age Differences in Alarm Call Response

Across studies, young responded more to alarm calls than adults; however, experimental and population details influenced the magnitude of difference between age classes. For example, the response variable measured influenced reported effect sizes; adults and juveniles respond more similarly to alarm calls when reactions are quantified in terms of time allocation rather than behavioral categories or flee response. It appears that younger animals are more likely to drastically change their behavior following a predator warning, but those that remain in exposed areas alter their time budgets similarly to adults. Young may be more reactive to alarm stimuli, but their time budgets (and the way they tradeoff foraging vs. vigilance) are comparable to that of mature individuals. Unfortunately, this relationship is confounded by taxa, in that almost all of the time allocation results (13/14) are from studies of squirrels. We encourage future investigators to quantify behavior with continuous, rather than categorical or binary, measures to facilitate future meta-analyses and provide a more precise estimate of behavior.

Although our meta-analysis is limited by the lack of biodiversity in available studies, our results suggest that the length of an animal's ontogenetic

period (in terms of absolute number of days) has important consequences for its antipredator behavior development. While animals that mature later in life (e.g., primates) often rely on mothers for locomotion, protection, and food during early development, quickly maturing species (e.g., squirrels) must spend their juvenile period independently foraging to grow and survive. Juvenile ground squirrels must balance predation threats with nutritional demands, because those that fail to gain sufficient mass during the active season will perish overwinter (Murie & Boag 1984). Since antipredator behavior and foraging are traded off within an individual's time budget, a juvenile that increases its vigilance or flees following an alarm call will lose valuable foraging time. Therefore, quickly maturing (and especially hibernating) species may display adult-like antipredator behavior early in life, because young must independently balance nutritional demands and predation threats.

In contrast, slowly maturing species (mature at age 1–3 or >3 yrs) are not required to independently forage or grow rapidly during their first months of life, and the cost associated with increased antipredator behavior is therefore reduced. In the absence of a nutritional cost, we may expect selection for these young mammals (who typically experience higher mortality than adult age classes, Caughly 1977) to be more responsive to risks than adults.

Although our results are consistent with the view that young display age-appropriate antipredator behavior, we cannot rule out the hypothesis that learning, experience, and physical development (e.g., of sensory, endocrine, or motor systems) shape juvenile antipredator behavior. The two hypotheses of age-related differences in antipredator behavior are not mutually exclusive, and it is likely that physiology, experience, and age-specific selective pressures explain variation in antipredator behavioral development.

Slowly maturing species (age at sexual maturity 1–3 or >3 yrs) may rely on learning and experience more so than quickly maturing species (age at sexual maturity < 1), and therefore display less adult-like behavior early in life. Slowly maturing young have more time to hone antipredator skills before living independently and may benefit from an increased reliance on learning and experience. By developing behavior through learning and experience, rather than relying on a fixed ability to respond appropriately to alarm calls on first exposure, young can fine tune their behavior to current predation risks and environmental conditions (Hollen & Manser 2006).

Future Directions

To fully evaluate the proposed hypotheses of ontogeny and antipredator behavior development, more studies of age-related differences, especially in unaddressed taxa, are needed. Our conclusions are somewhat limited owing to a lack of taxonomic diversity and the low number of studies reporting statistics appropriate for a meta-analysis (i.e., effect size measures, F, t, χ^2, $\bar{x}$ and variance data, or exact p-values). Our meta-analysis synthesizes all available data on the topic, but more studies are needed to tease apart the relative contributions of age-specific selection pressures (Hypothesis 1) vs. inexperience and immaturity (Hypothesis 2). Although the two hypotheses are not mutually exclusive, few attempts have been made to assess their relative influence; furthermore, we believe this hypothetical framework could be very useful for organizing future research on the ontogeny of alarm call response. Here, we discuss specific experiments and population comparisons that would greatly enhance explanations of maturation rate and age-related differences in antipredator behavior.

Hypothesis 1:

Age-specific selective pressures select for age-specific behavioral strategies (Cheney & Seyfarth 1983; Owings & Loughry 1985; Hanson & Coss 2001). Young display antipredator behavior that is adaptive for their age class, and the nature of age-specific selection pressures may vary among species with different life history characteristics and ontogenetic period lengths.

Within-species comparisons of populations with different age-specific predators or predation rates would greatly add to our understanding of age-specific selection pressures and subsequent age-specific strategies. If species that inhabit sites with predators that preferentially target juveniles are more responsive to alarm calls than species at sites *without* this sort of predator pressure, we may infer that differential selection pressures do in fact influence age-specific responses. Similar studies could be carried out *intraspecifically* and quantitative genetics could be used to estimate the magnitude of selection on antipredator behavior for young and adult age classes. Such quantitative genetic analyses would require continuous traits, and we therefore encourage future studies to focus on measures of time allocation rather than binomial or categorical responses. We suggest that studies linking selection/fitness and

antipredator behavior across age classes are potentially the most valuable for disentangling the two hypotheses of age-related differences in antipredator behavior.

The results of this meta-analysis support the hypothesis that young of quickly maturing (and especially hibernating sciurid) species display adult-like antipredator behavior early in life; this is perhaps because quickly maturing juveniles must independently forage (to meet intense nutritional demands) while avoiding predators. Young of slowly maturing species may be more vigilant than conspecific adults, because, in the absence of selection for rapid weight gain, age-specific predation rates may encourage heightened antipredator behavior in the more vulnerable age class. Future studies should attempt to disentangle the relationship between fast vs. slow maturation and age-specific selection related to nutritional demands by targeting species with specific life histories. For example, we may expect non-hibernating, quickly maturing species to behave quite differently than adults early in life; presumably, young of such species could allocate more time to vigilance without jeopardizing overwinter survival.

Hypothesis 2:

Young must develop their antipredator behavior. Until this development is complete, young may act differently than adults owing to their immature anatomy, neurology, or locomotive abilities. Furthermore, young may lack the experience or learned responses of adults and therefore act inappropriately during a predator encounter (Seyfarth & Cheney 1980; Hauser 1988). Young of slowly maturing species may therefore display less adult-like behavior early in life, because they have more opportunities for behavioral development than quickly maturing animals.

Although early studies attempted to study the influence of learning on behavioral development by rearing young in isolation (Herzog & Hopf 1984), isolation creates animals with a variety of behavioral problems that make it difficult to understand the effects of early experience on behavior (Bekoff 1976). Comparisons between captive and naturally reared young may provide a useful alternative. For example, Mateo & Holmes (1999) found that captive juvenile Belding's ground squirrels (who experienced artificially high levels of auditory, visual, and olfactory stimulation) were more responsive to alarm calls than conspecific young raised in the wild. Studies of this nature are crucial for understanding the influence of experience, early rearing environment, and learning opportunities on antipredator behavior development; however, their design must be extended to include adult age classes as well. We suggest similar studies of alarm call response in captive vs. wild juveniles *and* adults, so that the appropriate comparisons can be made. The findings of Mateo & Holmes (1999) suggest a role for experience in antipredator behavior development, but it is unknown whether increased experience promoted more adult-like behavior. Furthermore, studies with similar experimental designs that target quickly and slowly maturing species would allow us to address the relationship between ontogenetic period length and the degree to which experience influences behavioral development.

Studies of antipredator behavior following predator reintroductions (e.g., Gil-da-Costa et al. 2003) or exposure to novel predators in slowly vs. quickly maturing species will also be useful. If slowly maturing species use their long juvenile period to learn and fine-tune behavior to current environmental conditions, we may expect young of such species maturing in a 'new' predator environment to learn appropriate responses to the novel predator by the time they mature. Conversely, if young of quickly maturing species rely less on learning and experience during behavioral development, they may be more prone to erroneous antipredator behavior (e.g., incorrect predator classification; Seyfarth et al. 1980) in a novel predator environment.

Several studies have provided detailed descriptions of the ontogeny of alarm call responses in a single species (e.g., Mateo 1996; McCowan et al. 2001; Hollen & Manser 2006), but studies of additional species as well as a general framework are needed. Playbacks to young throughout their ontogenetic period could be used to construct developmental timelines with common milestones; such an approach would allow for clear comparisons across species. For example, when do young discriminate between alarm and non-alarm calls? When do young discriminate between different alarm call types? When do young act appropriately following functionally referential alarm calls? Construction of such structured timelines would allow us to specifically compare the role of immaturity/inexperience (via the tracking erroneous antipredator behavior) across species with different maturation rates.

We hope that these suggestions will guide future studies of alarm call response development. Our meta-analysis summarizes all current findings of

age-related differences in antipredator behavior, but our ability to tease apart the relative contributions of immaturity/inexperience vs. age-specific selection pressures is limited by the paucity of available studies. We encourage future studies of sex- and age-related differences in antipredator behavior, especially those designed to address current theories.

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Supporting Information

Additional Supporting Information may be found in the online version of this article:

Data S1. Effect size equations.

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