

Mate guarding and frequent copulation in birds: A meta-analysis of their relationship to paternity and male phenotype

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In many birds, males are presumed to protect their paternity by closely guarding their mate or copulating frequently with her. Both these costly behaviors are assumed to reduce the risk and/or intensity of sperm competition. However, despite many studies on avian extra-pair paternity, it remains unclear how strongly these behaviors are related to fitness and other key life-history traits. Here, we conduct meta-analyses to address two questions. First, are mate guarding and/or frequent copulation positively correlated with a male's share of paternity at his nest? We find a significant positive correlation between both presumed paternity protection behaviors and paternity share. The relationship is, however, weak ($r = 0.08\text{--}0.23$). This is perhaps unsurprising if the risk of partner infidelity, hence the need to protect paternity, varies among males. For example, more attractive males might have less need to protect their paternity. Second, do males with higher indices of so-called male "quality" (phenotypic measures, usually subjectively defined by researchers as predictors of male attractiveness) exhibit lower levels of paternity protection behavior? We find a negative correlation between male quality and paternity protection. This finding might partly explain the weak relationship between paternity protection and paternity, although we discuss other, nonmutually exclusive possibilities.

KEY WORDS: Copulation, guard, meta-analysis, paternity, quality.

Male behaviors that are presumed to protect paternity have likely evolved because they increase net male reproductive success (Parker 1970; Alcock 1994). In birds, it is assumed that males commonly use mate guarding and/or frequent copulation to protect their paternity (Møller and Birkhead 1991). Mate guarding occurs when a male remains close to his pair-bonded female, and appears to allow males to interfere with, or even prevent, extra-pair copulations (EPCs) by rival males (Westneat 1994; Currie et al. 1999). Male mate guarding includes following the female and spending a large proportion of time within a short distance of her (Birkhead and Møller 1992). For example, during the female's fertile period male bluethroats (*Luscinia s. svecica*) spend a larger

proportion of their time near their mate, and follow her more often than when she is no longer fertile (Krokene et al. 1996). In birds, mate guarding occurs predominantly during the female's fertile period (from 5 to 10 days before the first egg is laid, until the day the penultimate egg is laid; Birkhead and Møller 1992). Mate guarding is often most intense from 4 to 5 days before the first egg is laid until, depending on clutch size, the day the first egg is laid, or one or two days thereafter (Krokene et al. 1996; Foerster and Kempenaers 2005; Hoi et al. 2011).

Many species that mate guard also copulate more often than appears necessary for fertilization alone (Hunter et al. 1993; Hoi et al. 2011). Frequent copulation is often the sole putative paternity



protection in bird species where males are unable to guard their mates, for example, due to the simultaneous need for long feeding trips and nest defense (Møller and Birkhead 1991). In these species within-pair copulations often become more frequent during the fertile period (Barber and Robertson 2007; Hoi et al. 2011), although males of some species start to copulate frequently with their mate even before the fertile period (Villaroel et al. 1998). Copulation rates can be extremely high. For example, in tree swallows (*Tachycineta bicolor*) there are about 18 copulation attempts/hour during the presumed fertile period, and approximately five of these hourly attempts lead to cloacal contact (Crowe et al. 2009).

The apparent purpose of these two putative paternity protection behaviors is to avoid or reduce sperm competition. In birds, sperm competition has received much attention (Parker 1970; Birkhead and Møller 1998; Jennions and Petrie 2000; Simmons 2001; Alonzo and Pizzari 2013) since DNA-based paternity tests revealed the ubiquity of extra-pair paternity (EPP; (Griffith et al. 2002; Forstmeier et al. 2014). There are several hypotheses—some adaptive, others mechanistic or proximate—to explain variation in EPP among species, populations, and individual males (Westneat et al. 1990; Kempenaers et al. 1992; Hasselquist et al. 1996; Petrie and Kempenaers 1998; Westneat and Stewart 2003; Neudorf 2004; Akçay and Roughgarden 2007; see Table 1 for an overview and Forstmeier et al. 2014 for a recent review). Although many social and environmental factors affecting EPP have been considered (see Stutchbury and Morton 1995; Westneat and Sherman 1997; Møller and Ninni 1998; Griffith et al. 2002; Matysioková and Remeš 2014; Arct et al. 2015), one factor that has received little attention is how behaviors that are assumed to protect paternity relate to actual paternity. The most recent review we are aware of that relates behaviors associated with paternity protection across bird species to EPP is an 18-year-old meta-analysis (Møller and Ninni 1998).

Field studies often report considerable variation in how intensely individual males seem to protect their paternity, and some have attempted to relate this to the actual share of paternity at the nest (Dunn et al. 1994; Kempenaers et al. 1995; Møller and Tegelstrom 1997; Johnsen et al. 2003). Frequent copulation and mate guarding are likely to be costly behaviors (e.g., reducing foraging time; Lens et al. 1997; Komdeur 2001; Low 2006) suggesting they have compensatory benefits. The obvious benefit is to ensure paternity. Here, we perform a meta-analysis investigating the relationship between mate guarding and within-pair copulation rates and a male's share of paternity.

It has been widely assumed that females engage in EPCs for genetic benefits (reviews: Petrie and Kempenaers 1998; Jennions and Petrie 2000; Akçay and Roughgarden 2007) although there is little evidence for this claim (Forstmeier et al. 2014). A few high-

profile studies have documented greater expression in extra-pair than within-pair males of putative sexually selected traits thought to signal “quality” (e.g., Kempenaers et al. 1992). This is not a general trend: the estimated mean effect size for this difference did not differ from zero in a meta-analysis of 26 species (Hsu et al. 2015; see also Akçay and Roughgarden 2007). Ultimately, experimental manipulations of male traits are required to test whether females choose more ornamented males as extra-pair mates (e.g., Whittingham and Dunn 2016), but such experiments are rare.

This “good genes” hypothesis predicts that females paired to high-quality males are less likely to engage in EPCs (e.g., Kempenaers et al. 1992). This implies that high-quality males can afford to invest less in protecting their paternity. To test this claim, we ran a second meta-analysis of the relationship between male phenotypic quality and the two putative paternity protection behaviors. Using a male's phenotype as a measure of his “quality” (itself a surrogate for a high breeding value for fitness; see Hunt et al. 2004) can be subjective, but we follow the convention in the field and focus on male traits that researchers familiar with the natural history of their study species describe as being measures of quality or attractiveness (see Methods). This generally means sexually dimorphic, secondary sexual male traits that have been shown to correlate with aspects of male reproductive success (e.g., time to pairing, number of fledglings, nest success, number of mates). Unfortunately, few bird studies have experimentally manipulated traits to identify causal relationships with male mating/fertilization success (i.e., sexual selection), and even fewer studies can link any such traits to credible measures of male lifetime reproductive success as an index of fitness. The reader should bear in mind the weakness of this approach.

If male quality does not determine female decisions about EPCs, predictions of how male phenotype will relate to paternity protection behavior are unclear. Higher quality males may be better able to bear the costs of these behaviors, resulting in positive associations between quality and investment in paternity protection. This makes it difficult to predict the third relationship between the factors we consider: paternity protection, paternity, and male quality. That is, how are male quality and his share of paternity related? We do not provide a meta-analysis of this relationship, but we discuss the implications of our current findings for the link between male quality and paternity.

We acknowledge the limitations of analyzing phenotypic correlations to draw causal inferences. Even so, we believe it is possible to combine our results for the two reported relationships with information in the current literature to suggest biologically plausible relationships between the factors of interest. Based on the existing literature (e.g., Møller and Birkhead 1991; Akçay and Roughgarden 2007) we predict that:

Table 1. Overview of hypotheses referred to in the text for different aspects of within- and extra-pair paternity and EPCs.

Hypothesis or topic	Explanation, prediction	Reference
Good genes	A female should seek the best genes for her offspring by mating with a high-quality male, irrespective of whether this male is within- or extra-pair.	1, 2, 3, and 4
Genetic compatibility/similarity	Females seek genes for their offspring that are compatible with their own genes, or at least not incompatible (e.g., due to mating with a related individual).	4, 5, and 6
Other/direct benefits to female	A female may receive other benefits from extra-pair mating, for example, in the form of foraging opportunities, future mating, mate replacement, and additional paternal care.	7
Protect against infertility of social male	Females seek EPCs to protect against infertility of their social mate.	8 and 9
Mate guarding trade-off	A male has to “choose” how he divides his time between protecting his paternity, searching for extra-pair copulations and other essential activities, for example, feeding.	1
Male care trade-off	Males face a trade-off between caring for offspring and investing this energy in other activities, for example feeding or finding additional mating opportunities.	10
Female constraint	A male is expected to provide care to the offspring in response to his share of paternity or his certainty of paternity.	11
Breeding density/short NND	Short distances to other males or females increases EPC opportunities.	12 and 13
Breeding synchrony/asynchrony	Synchronous breeding allows females to find EPCs more easily. Alternatively, more asynchronous breeding can facilitate EPCs because males can protect their paternity and search for EPCs.	14
Polygyny	Polygynous males are expected to be unable to effectively protect their paternity with primary females, dependent on when the male attracts a secondary female.	1
Longevity	Long-lived species have long-term pair bonds and these are expected to be associated with greater fidelity.	15

References: 1, Westneat et al. 1990; 2, Jennions and Petrie 2000; 3, Mays and Hill 2004; 4, Akçay and Roughgarden 2007; 5, Brown 1997; 6, Arct et al. 2015; 7, Petrie and Kempenaers 1998; 8, Sheldon 1994; 9, Morrow et al. 2002; 10, Trivers 1972; 11, Westneat and Sargent 1996; 12, Møller and Birkhead 1993; 13, Westneat and Stewart 2003; 14, Stutchbury and Morton 1995; 15, Mauck et al. 1999.

- (1) There will be a positive relationship between within-pair paternity and copulation frequency or mate guarding intensity. That is, we assume that variation among males in other traits (e.g., risk of cuckoldry) does not overwhelm the inherent functional relationship between the use of putative paternity protection behaviors and a male increasing his share of paternity.
- (2) There will be a negative relationship between male quality and copulation frequency or mate guarding intensity. That is, more attractive males have less need to protect their paternity.

This search was performed using *ISI Web of Science* and was last updated on 1 January 2014. We used the key words “guard*,” “fertilization*,” “paternity,” or “copulation*,” within the following Web of Science categories: *Ecology*, *Zoology*, *Evolutionary Biology*, *Ornithology*, *Biology*, *Behavioral Sciences*, and *Multidisciplinary Sciences*. Additionally, we performed a forward search to locate papers that cited a previous meta-analysis on paternity studies by Møller and Ninni (1998). We did not attempt to find papers in other ways, or seek out unpublished datasets from colleagues. Our search yielded 20,882 unique references.

The references returned by these searches were initially assessed based on the journal name, title, and abstract (see Fig. 1 for an overview of the selection process). Papers on taxa other than birds or on an irrelevant topic were excluded (e.g., studies on “mammalian guard hairs”). We initially included studies with information on within- or extra-pair paternity and male quality even

Methods

LITERATURE SEARCH

The literature was searched for studies on two types of putative paternity protection: frequent copulation and mate guarding.

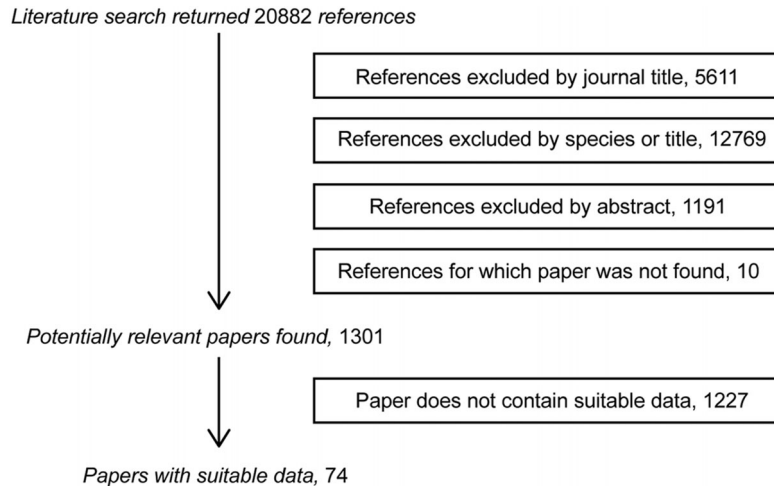


Figure 1. Flow diagram showing the paper selection process.

if paternity protection was not mentioned, as it became apparent that the required data were sometimes included in these papers. There were eight criteria for inclusion in the meta-analyses.

- (1) The publication reported the relationship between frequency of within-pair copulations and/or mate guarding and (a) paternity and/or (b) male “quality” (for definitions see *Data Extraction and Coding*).
- (2) The data were from socially monogamous or polygynous bird species that form pairs at a nest. For polygynous species the study had to report on the male’s primary nest. Other mating systems and pair types were excluded (e.g., cooperative breeding, polyandry, and polygamy).
- (3) The study was not performed with captive birds (i.e., in an aviary or on farmed birds).
The data were from a single breeding event for the population (e.g., the first breeding attempt in species with multiple clutches per season).
- (4) The data were from the fertile period. Where possible we only used data from the peak fertile period (~4 days prior to laying the first egg until the day before the last egg was laid). If this period was unavailable we used data from up to 10 days prior to laying the first egg until the day before the last egg was laid.
- (5) Paternity was determined by so-called “DNA methods” (see Griffith et al. 2002).
- (6) The paper contained appropriate statistics or raw data and sample sizes so that effect sizes and variances could be calculated.
- (7) The calculation of paternity was based on chicks per nest. For example, we exclude a case where the EPP was reported for the entire population per year (Korpimäki et al. 1996).

For 10 references we were unable to obtain the paper. However, only 74 of 1301 examined papers contained usable data (Fig. 1), so the likelihood that these 10 papers contained data that would alter the outcome of the meta-analysis is minimal.

DATA EXTRACTION AND CODING

We used the Pearson’s correlation coefficient (r) as our measure of effect size. When a study did not report a correlation but included other statistics, r was calculated from the reported statistics (e.g., mean \pm standard deviation [SD], t , F , P , R^2) using standard formulae (see Table S2 and Lipsey and Wilson 2001; Nakagawa et al. 2007; Borenstein et al. 2009; Koricheva et al. 2013). In order, our preference was for correlation coefficients (including Spearman’s rank, Kendall’s τ , and R^2); raw means with SDs; 2×2 frequency tables; statistics in the form of t , F , U , Wald, and Z ; calculating the mean and SD or a 2×2 frequency table from raw data in the text (including from tables or graphs); and finally from P -values (transformed to t). The r s were transformed to Fisher’s Z (Z_r) for analyses. We excluded results that were reported only as nonsignificant or “ $P >$.”

In a few instances several publications reported results for a species for the same year and population. To avoid overlapping data or duplicated results, we only allowed one paper to provide data for a population for a specific study period. We used the data from the paper that best matched our preference for the reported test statistic, or that was likely to include the most data.

These criteria yielded 74 papers that contributed 77 studies with 190 effect sizes for 45 species (see Table S1). “Paper” serves as an identity for a single publication per species (with one exception, Kempnaers et al. 1998 have data on two species and, for ease of analysis, each was given a separate paper identifier). “Study” identifies independent data published within a single paper, such as data from different years or populations. Conversely,

Table 2. Overview of the number of papers, studies, species, and effect sizes for both questions for different measures of paternity protection.

		Number of papers	Number of studies	Number of species	Number of effect sizes	
All		74	77	45	190	
Paternity	All	46	46	32	81	
	Guard	28	28	24	51	
	Manipulation	12	12	11	15	
	Copulation	14	14	12	15	
Male quality	All	40	42	28	109	
	Guard	Age	16	16	12	26
		Color	6	8	3	18
		Hormone	2	2	2	4
		Polygyny	6	5	5	11
		Size	12	12	9	31
		Song	5	5	4	7
		Manipulation	—	—	—	—
		Copulation	11	11	10	12
	Manipulation	Age	1	1	1	1
		Color	1	1	1	1
		Polygyny	5	5	5	6
		Size	4	4	3	4

data in separate papers from the same population in the same year, but addressing different questions or measures, were assigned the same study identity to account for nonindependence (there is only one case: Kempenaers et al. 1992, 1995).

For each reported measure of the relevant relationship we calculated an effect size. We calculated separate effect sizes for different years or populations. Thus, a paper could contribute multiple effect sizes for a particular type of relationship. Measures of putative paternity protection were grouped into three categories: mate guarding, copulation frequency, and “manipulations of paternity protection.” *Mate guarding* comprises measures such as the mean distance between the social pair, or the proportion of time spent together/apart. *Copulation frequency* is the within-pair rate of copulation. *Manipulations of paternity protection* were used in several studies. The most frequently used method was to temporarily remove a paired male, lowering his ability to guard or copulate frequently with his mate.

Depending on the study, *Paternity* was presented as within-pair and/or extra-pair paternity at the male’s nest. We adjusted the sign of the measure so that more within-pair or fewer extra-pair offspring in a clutch equates to higher values for paternity.

Male quality was measured in a variety of ways across and within papers, using different traits. We grouped these different measures into the following categories: age, color, hormone, polygyny, size, or song. *Age* measures were either male age in years, or male age class, because in many species it

is only possible to distinguish between young and older males. *Color* includes different measures such as hue and brightness, experimental manipulations of color or the use of color bands that affect male attractiveness. *Hormone* is a measure of testosterone levels and includes manipulations using testosterone implants. *Polygyny* distinguishes between males that have attracted one (monogamous) or multiple (polygynous) females. *Size* includes measures of mass, body or ornament size, and body condition. Finally, *Song* is a measure of male acoustic output. In general, the authors of the original study considered these traits to be signals of male quality/attractiveness.

Table 2 reports the number of papers, studies, species, and effect sizes per question. The direction of the effect sizes is such that a positive value indicates that: (1) higher levels of putative paternity protection behaviors are associated with higher paternity; and (2) higher quality males performed these behaviors more intensively. Note, however, that we predict a negative correlation based on the assumption that higher quality males have a lower risk of being cuckolded.

Our method sometimes resulted in multiple effect sizes for the same relationship from a single study. For example, a study could look at the relation between age and several measures of mate guarding (e.g., one effect size for distance between social pair and another effect size for time together). We used two approaches to handle nonindependent data. First, we ran a standard random-effects meta-analysis, which required that each

study contribute a single effect size. For this we calculated a single weighted mean effect size per study for each analysis (using a within-study meta-analysis). Second, we used a multilevel random-effects meta-analysis, which allowed for the use of multiple, nonindependent effect sizes by including the random factors “study” and “species” in the model. We also control for phylogenetic nonindependence. The type of male quality or putative paternity protection behavior was included as a fixed moderator.

We calculated the variance in Z_r as $1/(N-3)$, where N is the number of breeding pairs. In Table S1 we also include information on four other moderators used in our analyses: species, year of publication, and paper and study identity. For 18 effect sizes, we could calculate an effect size but not determine its direction. This was always associated with statistically nonsignificant results. In an attempt to control for the uncertainty introduced by directionless effect sizes we took a three-step approach with increasingly conservative assumptions. First, we excluded directionless effect sizes from the analysis (dataset 1). Second, if the first analysis revealed a significant mean effect we included the directionless datapoint(s) but used $r = Z_r = 0$ as the effect size (dataset 2). Third, if the analysis was still significant we assigned directionless effect sizes the direction opposite to that predicted (i.e., we assigned a negative direction for the paternity protection behavior–paternity relationship, and a positive direction for the paternity protection behavior–male quality relationship; dataset 3).

STANDARD RANDOM-EFFECTS META-ANALYSES

Separate random-effects meta-analyses were conducted for each question. Each study contributed one (weighted) effect size per analysis. For each question, a meta-analysis was conducted across all the categories combined (all) and then for each individual category (e.g., for “all” putative paternity protection behaviors and then separately for mate guarding, manipulation of paternity protection, and copulation frequency). But we did not run separate analyses for categories with fewer than four effect sizes.

We used a restricted maximum-likelihood method to estimate τ^2 (the true between-study variance). Studies on research questions in ecology and evolution have sometimes been found to yield diminishing effect sizes over time (e.g., Jennions and Møller 2002), so meta-regression was used to determine the effect of publication year on each of our questions, for all categories combined (all) and then separately for each category. We ran these meta-regressions separately to test for differences among the categories of paternity protection or male quality. We used Cochran’s Q statistic and I^2 to estimate heterogeneity in effect sizes.

MULTILEVEL (PHYLOGENETIC) RANDOM-EFFECTS META-ANALYSES

In the multilevel meta-analyses studies we included all effect sizes for each question by using species and study as modera-

tors. This method implicitly assumes that effect sizes extracted from the same study are statistically independent, that is, there is no within-study correlation between effect sizes, $r = 0$ (see Booksmythe et al. 2016), so we also ran the models assuming a more conservative correlation between effect sizes of $r = 0.5$ (see Tables S3 and S4). Note that the results assuming no within-study correlations are qualitatively very similar to those that do (compare Tables 6 and 7 to Tables S3 and S4). We used Bayesian Markov Chain Monte Carlo (MCMC) linear mixed-effects models to determine the overall effect size. For each of our two questions we ran four multilevel models: (1) a null model, with species and study as random effects; (2) a multilevel meta-regression, which added two moderator variables (publication year and category) to the null model; (3) a phylogenetic null model, which added information on phylogenetic relationships to the null model (i.e., Model 1); and (4) a phylogenetic meta-regression, which added phylogeny to the multilevel meta-regression model (i.e., Model 2). Models 2 and 4 were run without the intercept to directly obtain the mean estimates for the fixed effects. We ran models that included a phylogeny twice, using two different phylogenetic trees (the Ericsson tree and the Hackett tree: birdtree.org, Jetz et al. 2012; see Figs. S1 and S2). In the main tables and figures we present the results for the Ericsson tree. The results for the Hackett tree are in Tables S5–S7 and were quantitatively similar.

We used an inverse Gamma prior ($V = 0.002$ and $nu = 1$) for the random effects in all our multilevel models. The models were run for 1,100,000 iterations with a burn in of 100,000 iterations and a thinning interval of 1000. We calculated a modified P statistic to estimate heterogeneity (Nakagawa and Santos 2012). We report phylogenetic heritability, H^2 , as an index of the phylogenetic signal.

PUBLICATION BIAS

To test for publication bias we visually inspected funnel plots of the relationship between effect sizes and their precision ($1/SE$). Variance in the observed effect sizes should decrease with increasing sample size (lower sampling error) and this pattern should be symmetric. Asymmetry indicates potential publication bias (Jennions et al. 2013). We also used Egger’s regression (Egger et al. 1997) to statistically test for asymmetry. We used the trim-and-fill method (Duval 2005) and calculated a fail-safe N (Rosenberg 2005) as further tests of the robustness of our results to publication bias. These tests were performed on the data excluding directionless effect sizes (i.e., dataset 1). For the multilevel meta-analyses the model residuals were used in these tests.

All statistical analyses for the standard random-effects meta-analyses and bias detection were conducted in *R* using the *metafor* package (Viechtbauer 2010). For the multilevel random-effects

meta-analysis we used the *MCMCglmm* package in *R* (Hadfield 2010; Hadfield and Nakagawa 2010).

Results

STANDARD RANDOM-EFFECTS META-ANALYSES

Paternity protection and paternity

Behaviors assumed to increase paternity were significantly positively related to actual paternity when looking at all measures of paternity protection combined, and when looking separately at mate guarding or manipulation of paternity protection (Fig. 2A, Table 3). There was, however, no relationship between copulation frequency and paternity (Table 3). These findings were robust to the use of more conservative datasets (datasets 2 and 3), except that the relationship between mate guarding and paternity became nonsignificant ($P = 0.057$) for the most conservative dataset (Table 3).

Paternity protection and male “quality”

When we combined measures of paternity protection we found that higher quality males invested significantly less in paternity protection behaviors (Table 3), although using the more conservative dataset the relationship became nonsignificant ($P = 0.053$ in dataset 2, Table 3). Considering mate guarding and copulation frequency separately, we found that although high-quality males guarded significantly less, intriguingly they copulated significantly *more* frequently with their mates (Table 3, Fig. 2B).

We ran separate meta-analyses for the relationship between measures of paternity protection and the male quality categories that contained sufficient data. Mate guarding was significantly negatively related to *color*, *polygyny*, and *song* (Fig. 2B, Table 3), although the effect for *color* was not significant with the more conservative dataset (Table 3). The relationships between mate guarding and male *size* and *age* were not significant (Table 3). Copulation frequency was not related to *polygyny*, although its relationship with male *size* was significantly positive (Table 3). Larger males copulate more frequently with their mates.

Heterogeneity and publication bias

The heterogeneity (I^2) in effect sizes (Table 3) was low to moderate for the relationship between putative paternity protection behaviors and paternity, and moderate to high for most of the tested relationships between paternity protection and male quality (Table 3). For the relationship between paternity protection behaviors and paternity, the year of publication explained a significant proportion of the heterogeneity when combining all measures of behavior, and for the relationship with copulation frequency (Table 4). More recently published articles had more positive effect sizes. For the various relationships between paternity protection behavior and measures of male quality, the

year of publication affected only the relationship between mate guarding and *age* (earlier publications had smaller effect sizes; Table 4).

Inspection of the funnel plots revealed varying levels of asymmetry in our analyses (Fig. S3). Calculating the fail-safe number suggested that publication bias is of potential concern for about half of the significant relationships (six out of 11; Table 5), if we apply the criterion that $FSN < 5k + 10$ implies that a significant result is not robust (k is the original number of effect sizes; Rosenberg 2005). Egger's regression indicated a publication bias for studies of the relationship between paternity and mate guarding, and the relationship between copulation frequency and *polygyny* (Table 5). However, in neither case did trim-and-fill identify “missing studies.” Trim-and-fill did, however, identify missing studies for the relationships between mate guarding and *age*, mate guarding and *song*, and copulation frequency and *size* (Table 5). Correcting for these putative missing studies resulted in mean effect sizes of greater absolute value, but did not qualitatively alter our results (Table 5).

MULTILEVEL (PHYLOGENETIC) RANDOM-EFFECTS META-ANALYSES

The results of the multilevel random-effects meta-analyses (Table 6) were largely in agreement with those of the standard meta-analyses (see Table 3, analyses using “all” measures combined). Multilevel Model 1 confirmed that males that more often engage in behaviors assumed to protect paternity gained a greater share of paternity (Fig. 2A). However, the trend for higher quality males to engage in these behaviors less often was nonsignificant in multilevel Model 1 (Fig. 2B).

Model 2 estimated the effects of different trait categories as moderators. These can be compared to the results of the standard random-effects meta-analyses for individual categories (compare Table 7 to Table 3; Fig. 2). Again, the standard and multilevel approaches yielded similar results. However, in contrast to the standard model, in multilevel Model 2 we found that older males engaged significantly less than younger males in paternity protection behaviors. The relationship between mate guarding and *color*, which was significantly negative in the standard meta-analysis, was not significant in multilevel Model 2. Because copulation frequency did not have a significant relationship with male quality we did not test for variation among different male quality categories.

Phylogenetic results

In general, inclusion of the phylogenies did not greatly change the model outcomes (compare Model 1 to Model 3, and Model 2 to 4; Tables 6 and 7, respectively). In some cases, where the confidence interval boundary was close to zero for Models 1 and

Table 3. Results from the random-effects meta-analyses: Paternity protection in relation to paternity and traits putatively associated with male quality.

	Trait 1	Trait 2	Dataset	k	m	n	Mean (<i>r</i>)	L. CI	U. CI	z-value	P (z)	Q	df(Q)	P (Q)	<i>I</i> ² (%)
Paternity	All	1	1	43	31	1144	0.183	0.089	0.274	3.776	0.000	74.45	42	0.001	40.54
		2	2	46	32	1199	0.168	0.078	0.255	3.641	0.000	76.39	45	0.002	38.15
		3	3	46	32	1199	0.162	0.070	0.251	3.423	0.001	79.68	45	0.001	40.60
Guard	Guard	1	1	25	23	509	0.166	0.027	0.299	2.334	0.020	42.42	24	0.012	42.41
		2	2	28	24	564	0.134	0.010	0.253	2.117	0.034	43.28	27	0.025	35.51
		3	3	28	24	564	0.124	-0.004	0.249	1.903	0.057	45.78	27	0.013	39.34
Manipulation	Copulation	1	1	12	11	335	0.228	0.066	0.378	2.742	0.006	22.80	11	0.019	50.31
		1	1	14	12	300	0.084	-0.043	0.208	1.299	0.194	13.04	13	0.445	6.06
		1	1	36	23	1339	-0.187	-0.349	-0.013	-2.110	0.035	184.32	35	0.000	83.68
Male quality	Guard	2	2	42	28	1460	-0.153	-0.300	0.002	-1.938	0.053	199.19	41	0.000	81.14
		1	1	32	19	868	-0.275	-0.429	-0.105	-3.131	0.002	154.33	31	0.000	82.49
		2	2	38	24	976	-0.241	-0.379	-0.093	-3.152	0.002	159.51	37	0.000	78.80
Age	Color	3	3	38	24	976	-0.211	-0.358	-0.053	-2.614	0.009	171.23	37	0.000	80.89
		1	1	14	11	423	-0.294	-0.548	0.010	-1.901	0.057	72.43	13	0.000	88.34
		1	1	6	1	81	-0.278	-0.487	-0.038	-2.260	0.024	1.24	5	0.941	0.00
Polygyny	Size	2	2	8	3	139	-0.155	-0.327	0.027	-1.673	0.094	3.55	7	0.830	0.00
		1	1	5	5	139	-0.418	-0.552	-0.263	-4.950	0.000	1.74	4	0.783	0.00
		1	1	9	6	203	0.040	-0.284	0.357	0.237	0.813	28.91	8	0.000	76.57
Song	All	1	1	5	4	137	-0.423	-0.705	-0.024	-2.070	0.039	17.09	4	0.002	78.71
		1	1	11	10	296	0.334	0.115	0.523	2.930	0.003	32.91	10	0.000	70.07
		1	1	5	5	143	0.129	-0.137	0.378	0.954	0.340	8.78	4	0.067	55.25
Copulation	Size	1	1	4	3	83	0.414	0.006	0.705	1.986	0.047	7.42	3	0.060	63.66

Trait 1 gives the category of paternity protection and Trait 2 the category of male quality where applicable. *k*, the number of effect sizes; *m*, the number of species; *n*, the number of broods. L. CI and U. CI are the lower and upper 95% confidence intervals, respectively, for the estimated mean effect size. Confidence intervals that exclude zero are shown in bold.

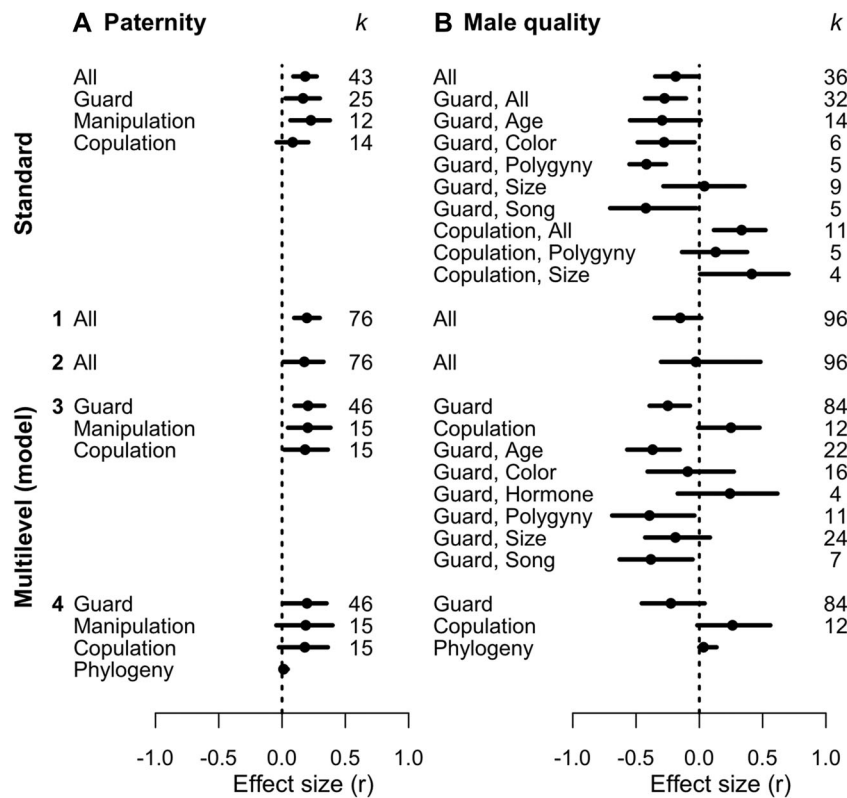


Figure 2. Forest plots of the meta-analytic means for (A) paternity and putative male “quality.” “Standard” refers to the results from the standard random-effects meta-analyses and “Multilevel” refers to the results from the four models for multilevel (phylogenetic, Ericsson phylogeny) random-effects meta-analyses. See the main text for a description of the categories. *k*, the number of effect sizes.

2, the inclusion of a phylogeny altered the estimate so that the boundary fell on the other side of zero in Model 3 or 4.

Heterogeneity and publication bias

Table 6 shows the variance not attributable to sampling error for Models 1 and 3. Table 7 shows for Models 2 and 4 the variance that can be attributed to differences between studies (I^2_{study}), species ($I^2_{species}$), and effect sizes ($I^2_{effect\ size}$); and, for Model 3, the variance due to the phylogeny ($I^2_{phylogeny}$). For Model 3 we also measured the phylogenetic signal (H^2 , Tables 6 and 7), which estimates how much variation is explained by the phylogeny. Meta-regressions showed that year of publication did not explain a significant amount of heterogeneity in Models 2 and 4, with the exception of the phylogenetic meta-regression (Model 4) for the relationship between putative paternity protection behaviors and paternity (Table 7).

Egger’s regression tests based on model residuals did not indicate asymmetry in the distribution of effects for the multilevel meta-analyses (see funnel plots, Fig. S4), and the FSNs suggest these results are robust to publication bias (Table 8). For the relationship between paternity protection behavior and male quality a trim-and-fill analysis identified 11 missing studies on the left side in both the phylogenetic and nonphylogenetic

models. However, adjusting our estimates to account for these putative missing studies still did not result in a mean effect that differed significantly from zero (Table 8). Trim-and-fill did not identify missing studies in the models for any of the relationships between putative paternity protection behaviors and paternity.

Discussion

We estimated mean effect sizes for the relationships between paternity protection behaviors and paternity, and paternity protection behaviors and male quality, using standard and multilevel random-effects meta-analyses. The two approaches always agreed on the mean direction of the effect, although sometimes one approach reported a significant effect whereas the other yielded a marginally nonsignificant one. We discuss the patterns separately for each relationship based on the general consensus from the models.

DO PRESUMED PATERNITY PROTECTION BEHAVIORS PREDICT ACTUAL PATERNITY?

In general, behaviors described as forms of paternity protection are significantly positively correlated with actual paternity. The mean correlation is, however, weak (mean $r = 0.18$ for “all” behaviors). Individually, both mate guarding ($r = 0.17$) and

Table 4. Meta-regression results for the effect of year of publication from the random-effects meta-analyses: Paternity protection in relation to paternity and putative male quality.

	Trait 1	Trait 2	Q_1	P	$B_{(\text{year})}$	L. CI	U. CI
Paternity	All		7.291	0.007	0.123	0.034	0.211
	Manipulation		2.092	0.148	0.127	-0.045	0.292
	Guard		2.174	0.140	0.106	-0.035	0.241
	Copulation		5.083	0.024	0.138	0.018	0.255
Male quality	All		0.228	0.633	-0.041	-0.209	0.128
	Guard	All	0.542	0.462	-0.064	-0.229	0.106
		Age	6.071	0.014	-0.311	-0.520	-0.066
		Color	0.358	0.550	0.135	-0.300	0.523
		Polygyny	0.587	0.444	-0.074	-0.256	0.114
		Size	0.334	0.563	0.093	-0.217	0.386
		Song	0.030	0.863	0.048	-0.461	0.533
	Copulation	All	1.967	0.161	0.158	-0.063	0.364
		Polygyny	0.248	0.618	0.088	-0.252	0.409
		Size	0.149	0.699	0.123	-0.467	0.638

Trait 1 gives the category of paternity protection behavior and Trait 2 the category of male quality where applicable. L. CI and U. CI are the lower and upper 95% confidence intervals, respectively, for the effect of year. Confidence intervals that exclude zero are shown in bold.

manipulations of paternity protection, for example male removal ($r = 0.23$) are significantly positively correlated with paternity. Males that guard less, or that have been removed or confined during the fertile period, had significantly lower within-pair paternity. In contrast, the mean relationship between frequent copulation and paternity is not significant ($r = 0.08$).

Paternity protection behaviors are seemingly costly. Mate guarding increases energy expenditure, reduces feeding opportunities, and can elevate predation risk (Birkhead and Møller 1992; Komdeur 2001; Cooper and Vitt 2002; Low 2006; Ancona et al. 2010; Rodríguez-Muñoz et al. 2011). Similarly, copulating frequently is likely to be energetically costly (Birkhead and Møller 1992; Lens et al. 1997), might reduce the vigilance of pair members (Hunter et al. 1993), and could increase the risk of acquiring a sexually transmitted infection (Lombardo et al. 1996; Stewart and Rambo 2000) although the risks are presumably smaller when copulating with the same partner. Given these costs there must be a compensatory benefit. Our results suggest that the costs are offset by an increased share of paternity. It might seem obvious that the effort a male puts into paternity protection will relate to his actual paternity. This is not necessarily the case, however, as paternity also depends on a female's cooperation (Birkhead and Møller 1993; Lifjeld et al. 1994; Petrie and Kempenaers 1998). Female control of paternity can arise by, for example, active pursuit of EPCs or selective sperm ejection after mating (Birkhead and Møller 1993; Lifjeld et al. 1994; Pizzari and Birkhead 2000; Westneat and Stewart 2003). If a female is unlikely to pursue EPCs her social mate's paternity could remain high even if he is poor at mate guarding or copulates infrequently. Variation in female propensity to pursue EPCs could weaken the relationship

between paternity protection behaviors and actual paternity. Additionally, males might adjust their level of paternity protection in direct response to female quality if it is linked to her fecundity or offspring reproductive value (Clutton-Brock 2009).

In addition to female choice, paternity can be influenced by a range of biological factors that were generally unaccounted for in the studies included in our analysis, such as sperm traits (Froman et al. 2002), and environmental and demographic factors (Rowe and Weatherhead 2007; Yuta and Koizumi 2016). For example, high local breeding density (Westneat and Sherman 1997; Møller and Ninni 1998; Griffith et al. 2002; Mougeot 2004; Neudorf 2004) and breeding synchrony (Stutchbury and Morton 1995; Stutchbury 1998; Møller and Ninni 1998; Neudorf 2004; but see Westneat and Sherman 1997; Weatherhead and Yezerinac 1998) are expected to increase EPCs, hence EPP, simply by providing more ready access to potential extra-pair mates. Similarly, nearest-neighbor distance (e.g., Mougeot 2004) and local adult or operational sex ratio might influence the value of paternity protection behaviors in terms of elevating paternity (Weir et al. 2011; Harts and Kokko 2013). If these factors vary among breeding pairs in the sample, they will weaken the relationship between putative paternity guarding behaviors and actual paternity. Logistical challenges could also weaken reported effect sizes. High plasticity of behavioral traits can lead to low repeatability (Bell et al. 2009), impeding accurate estimates of mean trait values, especially given the often limited sampling in field studies. Behavioral traits can be difficult to measure precisely, introducing additional statistical noise due to measurement error. These extenuating biological factors and methodological limitations can potentially reduce effect sizes, and could explain the weak relationship observed between

Table 5. Results for estimates of Fail-safe N (FSN), Egger's regression tests, and trim-and-fill (TAF) tests for the random-effects meta-analyses: Paternity protection in relation to paternity and putative male quality.

Paternity	Trait 1	Trait 2	Fail-safe		<i>t</i> , Egger's	Df(t)	P(t)	Missing k: TAF	Mean (r)	L. CI	U. CI	z-value	P(z)	Q	df(Q)	P(Q)	I ² (%)
			N	N													
Paternity	All		173		1.513	41	0.138	0									
	Manipulation		49		-1.115	10	0.291	0									
	Guard		1		2.860	23	0.009	0									
	Copulation		0		0.539	12	0.600	0									
Male quality	All		303		0.397	34	0.694	0									
	Guard	All	450		-0.194	30	0.848	0									
		Age	103		-0.249	12	0.831	5	-0.484	-0.677	-0.228	-3.497	0.001	136.56	18	0.000	90.58
		Color	2		0.390	4	0.716	0									
		Polygyny	27		0.076	3	0.944	0									
		Size	0		-0.888	7	0.404	0									
		Song	59		2.481	3	0.089	1	-0.546	-0.804	-0.117	-2.423	0.015	27.69	5	0.000	86.51
		All	72		0.297	9	0.773	0									
		Polygyny	0		4.528	3	0.020	0									
		Size	16		-0.799	2	0.508	2	0.621	0.232	0.839	2.901	0.004	18.5	5	0.002	78.31

Trait 1 gives the category of paternity protection and Trait 2 the category of male quality where applicable. Robust FSN are shown in bold. L. CI and U. CI are the lower and upper 95% confidence intervals, respectively, for the estimated mean effect size incorporating putative missing studies. Note that FSN = 0 when the effect was nonsignificant in the original analysis.

Table 6. Results from the multilevel meta-analyses (Ericsson phylogeny): Paternity protection in relation to paternity and putative male quality, for Models 1 and 3 (null model and phylogenetic null model, respectively).

M	Dataset	k	m	n	Mean (r)	L. CI	U. CI	I^2_{study} (%)	I^2_{species} (%)	$I^2_{\text{Effect size}}$ (%)	$I^2_{\text{phylogeny}}$ (%)	I^2_{total} (%)	H^2 (%)
Paternity	1	1	76	31	1144	0.196	0.298	20.49	14.20	11.83		46.52	
	2	1	81	32	1199	0.185	0.279	23.70	12.24	9.62		45.55	
	3	1	81	32	1199	0.180	0.275	27.75	11.33	9.08		48.17	
3	1	1	76	31	1144	0.176	0.327	17.77	11.87	10.60	10.03	50.26	23.73
	2	1	81	32	1199	0.166	0.288	19.76	10.39	9.41	9.59	49.15	21.30
Male quality	1	1	96	28	2262	-0.151	0.015	4.75	55.53	22.53		82.81	
	3	1	96	28	2262	-0.028	0.483	4.12	39.63	19.81	21.16	84.73	46.80

M, model; *k*, the number of effect sizes; *m*, the number of species; *n*, the number of broods. L. CI and U. CI are the lower and upper 95% confidence intervals for the estimate mean, respectively. Confidence intervals that exclude zero are shown in bold.

paternity and paternity protection behavior. If the true relationship is stronger, explaining paternity protection behaviors via their paternity-enhancing effects becomes easier. However, any link to the relationship between paternity protection and male phenotypic quality could become harder to explain (see below).

A previous meta-analysis reported nonsignificant relationships between mate guarding, copulation frequency, and paternity (Møller and Ninni 1998). The greater number of studies in our analysis gives us greater statistical power, likely contributing to the significant results we obtained for the effects of paternity protection on actual paternity. We also found, however, that more recent publications report more positive effect sizes for this relationship. There is no obvious explanation for this trend. One concern is the possibility that some studies remain unpublished or selectively report relationships due to a bias against statistically nonsignificant findings (Rosenthal 1979). This concern is partly assuaged by the observation that several studies reported the relationship between paternity protection and paternity as a secondary finding (e.g., Bjørnstad and Lifjeld 1997; Lifjeld et al. 1998; Buchanan and Catchpole 2000), which should reduce the risk of publication bias. On the other hand, many studies reported nonsignificant relationships in a way that prevented calculation of an effect size, hence their inclusion in our analyses (e.g., $P > 0.3$ or $P = \text{NS}$; Hoi et al. 2011). In addition, our calculation of fail-safe numbers suggests that, for the standard analyses, the number of “missing” studies with mean effect of zero needed to reduce the estimated mean effects for paternity–paternity protection relationships to nonsignificance is quite low, relative to the number of reported studies (Table 5). However, this is not the case for the multilevel analysis (Table 8).

HOW DOES MALE PHENOTYPE RELATE TO PATERNITY PROTECTION BEHAVIORS?

Given the widely invoked claim that females engage in EPCs for genetic gains, females are expected to prefer high-quality males as both within- and extra-pair mates (but see Hsu et al. 2015 for empirical evidence otherwise). We might therefore predict that, all else being equal, high-quality males invest *less* in protecting their paternity, because their mates are unlikely to solicit EPCs. This assumes that females actively solicit EPCs, which generally seems true (see Birkhead and Møller 1992; Hunter et al. 1993). However, in some species EPCs appear to be forced upon females (e.g., Alatalo et al. 1987; Morton 1987; Jones et al. 2012). If forced EPCs occur then females are expected to cooperate with mate guarding; and we might make the counterprediction that high-quality males will invest *more* into protecting their paternity due to, say, greater energetic reserves. Intriguingly, we found that although the relationship between the various measures of male quality and mate guarding is usually significantly negative, their

Table 7. Continued.

M	Dataset	k	Paternity protection	Mean (<i>r</i>)	L. CI	U. CI	<i>I</i> ² _{study}	<i>I</i> ² _{species}	<i>I</i> ² _{Effect size}	<i>I</i> ² _{phylogeny}	<i>I</i> ² _{total}	<i>H</i> ²	
Male quality	1	22	Age	-0.369	-0.570	-0.155							
			Color	-0.092	-0.409	0.273							
	Guard	4	Hormone	0.242	-0.171	0.617							
			Polygyny	-0.394	-0.689	-0.039							
	7	24	Size	-0.189	-0.428	0.084							
			Song	-0.383	-0.630	-0.053							
			Year	-0.041	-0.164	0.074	4.35	59.88	12.64				76.87
2	Guard	26	Age	-0.358	-0.534	-0.144							
			Color	-0.057	-0.351	0.243							
	4	18	Hormone	0.244	-0.165	0.596							
			Polygyny	-0.378	-0.654	-0.036							
	7	31	Size	-0.164	-0.362	0.070							
			Song	-0.370	-0.611	-0.042							
			Year	-0.033	-0.161	0.084	4.12	65.85	8.25				75.23
3	Guard	26	Age	-0.307	-0.503	-0.053							
			Color	0.025	-0.275	0.349							
	4	18	Hormone	0.237	-0.183	0.630							
			Polygyny	-0.363	-0.667	0.027							
	7	31	Size	-0.132	-0.386	0.103							
			Song	-0.409	-0.636	-0.043							
			Year	-0.011	-0.126	0.113	6.84	61.78	9.78				78.39
4	1	84	Guard	-0.225	-0.455	0.042							
			Copulation	0.262	-0.016	0.561	8.19	44.36	24.23				76.78
		12	Year	0.027	-0.081	0.135						50.38	

M, model; *k*, the number of effect sizes. L. CI and U. CI are the lower and upper 95% confidence intervals for the estimated mean, respectively. Confidence intervals that exclude zero are shown in bold.

Table 8. Results of Fail-safe number (FSN), Egger's regression tests, and trim-and-fill (TAF) tests for the multilevel meta-analyses.

	Model	Dataset	Fail-safe <i>N</i>	<i>t</i> , Egger's	<i>Df</i> (<i>t</i>)	<i>P</i> (<i>t</i>)	Missing <i>k</i> : TAF	Mean (<i>r</i>)	L. CI	U. CI
Paternity	1	1	547	0.938	74	0.351	0			
	3	1		0.874	74	0.385	0			
Male "quality"	1	1	904	0.379	94	0.706	11	-0.057	-0.121	0.008
	3	1		0.360	94	0.720	11	-0.056	-0.120	0.009

Paternity protection in relation to paternity and putative male quality for Models 1 and 3 (null model and phylogenetic null model [Ericsson phylogeny], respectively). Robust FSN are shown in bold. L. CI and U. CI are the lower and upper 95% confidence intervals, respectively, for the estimated mean effect size incorporating putative missing studies.

relationship with copulation frequency is significantly positive (Tables 3 and 7).

There are at least two potential explanations for the generally positive relationship between copulation frequency and male quality ("all" traits). First, frequent copulation might benefit males by ensuring fertilization, regardless of sperm competition risk. If high-quality males have larger energy reserves, they can afford to copulate more frequently. Second, females might solicit fewer copulations when paired with a low quality social male to reduce his share of paternity (Birkhead and Møller 1993; Hunter et al. 1993). Note, however, that the mean relationship between copulation frequency and actual paternity is nonsignificant (95% CI: -0.01-0.48). So, there is little direct evidence that high-quality males gain greater paternity through more frequent copulations.

Our results indicate that high-quality males spend significantly *less* time guarding their mates (Tables 3 and 7). Can they afford to do so because their partners are less likely to seek EPCs? Answering this question requires information linking both male and female behavior during the fertile period to male quality. Very few studies have explored this relationship. In the bluethroat, older males mate guard less but their females appear to cooperate by moving less often, suggesting that they do not actively seek EPCs (Johnsen et al. 2003). Higher quality males could thus reduce their mate-guarding intensity, instead investing in EPC attempts (Wagner et al. 1996). Conversely, low-quality males might mate guard intensively because they are unlikely to gain paternity elsewhere, while their own mates are more likely to accept EPCs (Kempnaers et al. 1995).

We looked at how mate-guarding intensity correlated with five categories of male quality: age, color, polygyny, size, and song. The sample size for each category was small (5-14 effects from one to 11 species), and only polygyny and song consistently showed significant negative relationships, whereas the relationships for age and color were marginally significant, depending on the model (Tables 3 and 7). There was no relationship between mate guarding and male size.

Polygyny in birds has been linked to reduced ability to guard a primary mate simply because a male cannot guard two females simultaneously ("trade-off hypothesis" see Table 1; Birkhead and Møller 1992; Hasselquist and Sherman 2001). Additionally, where females do prefer "high quality" males (Hasselquist and Sherman 2001), polygynous males should be more attractive so that their mates are less likely to seek EPCs, and therefore require less guarding. Our analysis suggests that within a given species polygynous males guard less than socially monogamous males. However, we cannot determine whether this pattern arises because polygynous males have less to gain from paternity protection, or because their time is more profitably spent attracting another mate, or because of the inherent time trade-off. Ideally, we need better data on when males attract a second female. If outside of the primary female's fertile period, it is unlikely to influence mate guarding. Of the six studies in our meta-analysis linking polygyny to mate guarding only three explicitly mention whether males tried to attract a second female during the primary mate's fertile period (Alatalo et al. 1987; Kempnaers et al. 1995; Pinxten and Eens 1997). The remaining studies assume that a male guards his primary female less because he is attracting another female (Kempnaers et al. 1992; Dunn and Robertson 1993; Pilastro et al. 2002).

Our finding that males that guard intensively sing less is consistent with the "male announcement of fertility hypothesis" (Table 1; Møller 1991), which claims that males that sing more have mates that are less likely to seek EPCs, and therefore require less guarding. Again, however, direct evidence linking song to male fitness was rare in the included studies. We also note that song duets are sometimes considered a form of mate guarding, in which case additional guarding behaviors would be redundant so that a negative relationship between song and guarding need not invoke a mediating role for male "quality." On the other hand, there is evidence in many well-studied bird species that duets are used to communicate with potential extra-pair mates (review: Dahlin and Benedict 2014). As such the causal link between song and paternity protection remains unclear.

What is “quality?”

We followed the original researchers in characterizing measured male phenotypic traits that they assume to be associated with male reproductive success as indices of quality. In many cases there is no strong evidence that the trait in question affects male reproductive fitness. That is, we lack experimental tests causally linking the trait to male mating success to show that it is sexually selected. In the case of polygyny it is simply assumed that male mating success is causally related to male quality and that stochastic events play little role in generating variation among males (but see Jennions et al. 2012). Even if the focal trait is sexually selected, an additional assumption that the trait is heritable is necessary for female choice for high-quality males (in the standard “good genes” sense; see Hunt et al. 2004) to be adaptive (review: Forstmeier et al. 2014).

It is worth considering how the relationships we found can be explained if the measured phenotypes do not reflect male attractiveness. As already mentioned, males that have the opportunity for polygyny may simply face a trade-off between guarding their first mate and attracting and attending to another female. Similarly, the trade-off between guarding and attracting extra-pair females might change with male age, with younger, inexperienced males gaining more from a guarding strategy while older males more successfully seek out EPCs.

RELATING PATERNITY, PATERNITY PROTECTION, AND MALE QUALITY

How should we integrate existing knowledge on paternity, paternity protection, male quality, and other factors influencing these traits? We illustrate some possible relationships schematically in Fig. 3.

Socially monogamous birds are presumed to reduce sperm competition by using putative paternity protection behaviors like mate guarding and frequent copulation. Bearing in mind that correlation is not causation, we show that these behaviors seem to be moderately effective at protecting paternity, based on the observed positive relationship. Given that these are costly behaviors we would, however, also predict that males use them less often when the benefits are smaller. In particular, investment into paternity protection seems less likely to be beneficial for preferred males. One potential link between the two relationships investigated here is that if EPC is adaptive, then by definition (ignoring researcher errors in identifying sexually selected traits) high-quality males are preferred mates. This implies that higher quality males should invest less into paternity protection. In general our results for mate guarding, but not frequent copulation, support the claim that high-quality males are under selection to use a strategy that is less protective. This raises a seeming paradox. Does the positive mean relationship between paternity protection behaviors and paternity imply that high-quality males gain less paternity? The

short answer is no. It is a general statistical rule, often overlooked, that knowing the pairwise correlations between a focal variable (here “paternity protection behavior”) and two others *does not* allow us to determine the correlation between those two variables (see Langford et al. 2001). We still need to directly quantify the relationship between male quality and paternity. In addition, the reported effect sizes are based on correlational data, with the exception of effect sizes for experimental manipulation of mate guarding. Interestingly, however, models in which both sexes’ behaviors evolve suggest that high-quality males can evolve to guard less than low-quality males, yet their realized paternity remains higher because their mates “need less convincing” to remain faithful (Kokko and Morrell 2005). Unfortunately, we lack the relevant data to conduct a meta-analysis linking female propensity to seek EPCs, to male “quality.”

There are at least three additional reasons why a negative relationship between paternity protection and male quality need not imply that high-quality males gain less paternity. First, the relationship between paternity and mate guarding is weak. Second, how paternity is measured could play a role: some studies only distinguish between full and partial paternity (e.g., Møller and Tegelstrom 1997; Chuang-Dobbs et al. 2001). Thus high-quality males could lose paternity but still, on average, have greater within-pair paternity than lower quality males. Third, high-quality males that engage in more EPCs might lose paternity in their own nest, but still have a higher total offspring count by siring offspring elsewhere (Webster et al. 1995; Neff and Pitcher 2005; Balenger et al. 2009; Cleasby and Nakagawa 2012).

The relationship between male quality and paternity has been covered in several reviews. Møller and Ninni (1998) found that paternity was significantly positively related to male age, secondary sexual characters, wing length, and survival, but negatively related to polygyny. A more recent meta-analysis found no significant correlation between male age and within-pair paternity (Cleasby and Nakagawa 2012). Although song has been positively related to paternity in several single-species studies (Hasselquist et al. 1996; Krokene et al. 1996; Gil et al. 2007; Hill et al. 2011), a meta-analysis and comparative analysis found no significant relationship (Garamszegi and Møller 2004). Akçay and Roughgarden (2007) reported a positive relationship between paternity and male age and size; but nonsignificant relationships with body condition and sexual secondary characteristics after correcting for possible publication bias. Most recently, Hsu et al. (2015) in a large meta-analysis showed there are few phenotypic differences between extra-pair and social males. In general, support for a positive relationship between male quality and within-pair paternity therefore seems quite weak. One counterargument is that researchers are measuring the wrong male traits (Kokko and Lindström 1996; Brooks and Kemp 2001; Arnqvist and Rowe 2005; Akçay and Roughgarden 2007). Ultimately, studies assume their

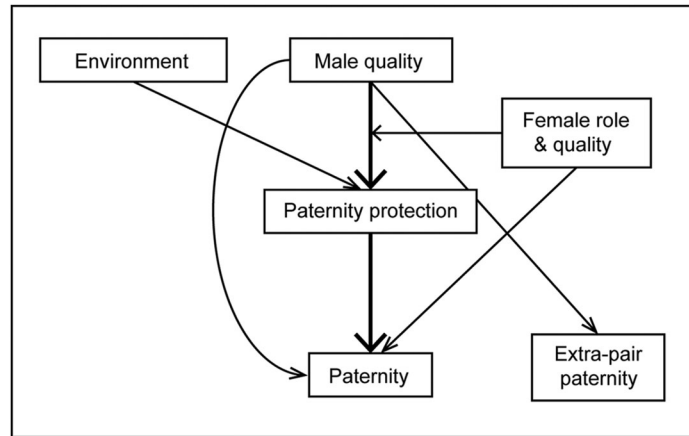


Figure 3. The interrelationships between factors discussed in relation to paternity. The thick black lines represent the two relationships that we directly addressed. The thinner black lines represent relationships from existing theory, comparative and meta-analyses. The details of the mitigating factors and interrelationships are discussed in the text.

focal traits are indicators of heritable variation in fitness (i.e., that these males will sire fitter offspring). Some traits may be more relevant than others. Researchers often measure many male phenotypic traits and then focus on those that are significantly correlated with mating success, or other indices of performance, as proxies for “quality.” Researchers may therefore reason backward from an underlying hypothesis that high male quality should predict certain outcomes to conclude that phenotypes that relate to the outcome of interest do so *because* they reflect male quality. Traits might be treated as quality indicators simply because they had a significant relationship with, for example, paternity or paternity protection. We again emphasize that many of these traits might not truly reflect “quality” (sensu Hunt et al. 2004). Our meta-analysis ultimately reveals that there are, on average, significant relationships between certain classes of phenotypic measure and paternity protection behavior in socially monogamous birds.

In conclusion, in socially monogamous birds presumed paternity protection behaviors are correlated with within-pair paternity, albeit quite weakly ($r = 0.18$). Furthermore, paternity protection behaviors are negatively correlated with male phenotypic traits often described as indices of “quality” ($r = -0.19$). However, considering mate guarding and frequent copulation separately reveals different patterns. While mate guarding is negatively correlated with quality ($r = -0.28$), frequent copulation is positively correlated ($r = 0.33$). Although many questions remain, our work highlights the role that paternity protection behaviors could play in generating variation in male reproductive success in wild bird populations.

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Supporting Information

Additional Supporting Information may be found in the online version of this article at the publisher's website:

- Figure S1.** The Ericsson backbone phylogenetic trees used for both questions.
- Figure S2.** The Hackett backbone phylogenetic trees used for both questions.
- Figure S3.** Funnel plots for both questions when using the random-effects meta-analyses.
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- Table S1.** Data extracted from literature.
- Table S2.** Formulae used for calculation of effect sizes from different types of statistics or data type.
- Table S3.** Results from the multilevel meta-analyses for both questions.
- Table S4.** Results from the multilevel meta-analyses for both questions (Hackett phylogeny).
- Table S5.** Results from the multilevel meta-analyses for both questions (Hackett phylogeny).
- Table S6.** Results from the phylogenetic multilevel meta-analyses (Hackett phylogeny) for both questions.
- Table S7.** Results of Egger's regression tests and trim-and-fill (TAF) tests for the multilevel meta-analyses (Hackett phylogeny).