

The interrelationships between resource-holding potential, resource-value and reproductive success in territorial males: How much variation can we explain?

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Abstract A long-standing hypothesis in behavioural ecology posits that males with greater resource-holding potential (RHP) control resource sites deemed more valuable by sexually-receptive females and, thereby, males controlling such sites accrue greater reproductive success (RS). This hypothesis has historically been investigated using three separate but non-mutually exclusive relationships (male RHP vs. resource value, resource value vs. male RS and male RHP vs. RS). The relationships between these three variables are predicted to be strongly positive, however, due to measurement error and biological noise, perfect correlations ($r = 1.0$) are rare in biology even for well-established relationships. Moreover, the inaccurate identification of either the male trait(s) important to RHP or the resource characteristic sought by females will weaken the observed strength of the relationships. Here, I use meta-analysis to quantitatively describe the general pattern of these relationships in animals. I predict that the relationships between male RHP, resource-value and RS

should be significantly positive (male RHP and resource-value should explain a large amount of the variation in male RS). My meta-analysis supports this hypothesis; however, in the best case scenario only ca. 20% of the variation in the response variable was explained. I conclude by identifying areas in which we need to improve our investigations of resource-defence animals and recommending approaches to meet these needs.

Keywords Resource-defence · Resource-holding potential · Resource value · Mating success · Sexual selection · Meta-analysis · Publication bias

Introduction

Breeding female animals require particular materials from the environment, such as oviposition or egg-laying sites, food and refugia from predators (Emlen and Oring 1977; Thornhill and Alcock 1983). If the resources critical to adult females are economically defensible by single adult males, for example by being spatially or temporally clumped, males can increase their fitness by controlling the resources and exchanging access to them for copulations (Emlen and Oring 1977; Brown et al. 1997). The greater the degree to which resources can be monopolized by males, the greater the variance in male reproductive success and the more intense the sexual selection on male traits favouring control of resources (Emlen and Oring 1977; Shuster and Wade 2003).

Sexually-receptive females should seek the best available resources if their fitness is tied to resource quality, as it often is (Møller and Jennions 2001a). There are six hypotheses explaining how females could assess resource value and decide to settle on particular resource sites or

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territories. These hypotheses assume that males always occupy the resources that the females need unlike, for example, in *Hemideina* tree weta where empty refuges are occasionally available to females (Kelly 2006c). First, females could choose based on resource value alone if resources are more readily assessed than male quality and if there is little possibility for male deceit about resource value (Searcy 1979). Moreover, if male-male competition for resources acts as a filter to male genetic quality then, by default, females should acquire a high-quality male on a high-value resource. Hence, Brown et al. (1997) suggest that females should be selected to assess resource value and if female mate choice exists, it should be exercised either during or after copulation, not before. It should also be noted that although females could accrue direct fitness benefits by choosing males based on phenotype (e.g. decreased risk of acquiring sexually transmitted diseases, Reynolds and Gross 1990; Kirkpatrick and Ryan 1991), these benefits should be small relative to effects of variation in resource value, particularly if the survival and mating success of a female's offspring are dependent upon the larval environment (e.g. Howard 1978b; Reaney and Backwell 2007).

Second, females could base their choice directly upon the male phenotype if the genetic benefits offered by a male are more critical to offspring fitness than resource value (Pomiankowski 1988) or if male characters indicate non-resource-based direct benefits such as the quality of paternal care (e.g. Downhower and Brown 1980).

Third, females could use male phenotype as a cue to resource value if contests over resources produces a positive association between male phenotype and resource quality (Howard 1978a; Gottlander 1987; Hoi-Leitner et al. 1995). Therefore, females could indirectly choose a high-value resource by mating with males possessing phenotypic indicators of greater resource-holding potential (hereafter RHP, Parker 1974). For example, controlled field experiments showed that female *C. s. xanthostoma* damselflies choose to mate and oviposit at particular locations based on the phenotype (degree of wing pigment heterogeneity) of the resident male (Siva-Jothy 1999). Given that resident males tend to also control better oviposition sites, females possibly gain the direct benefits of ovipositing on a higher-quality territory in addition to being guarded by a male that is better able to repel harassing conspecific males (Siva-Jothy 1999). Alternatively, if male genetic quality and resource value are not correlated, females would have the opportunity to choose sires independent of resources (Conrad and Pritchard 1992). For example, female *Calopteryx dimidiata* damselflies are able to separate mate choice and resource choice because females can mate with a high-quality male and then seek a superior oviposition site elsewhere; given that they oviposit underwater and therefore can submerge and lay eggs free from harassment

by the resident male (Waage 1984; see also Forsyth and Montgomerie 1987; Tsubaki and Ono 1987).

Fourth, females may use resource characteristics as a cue to male quality. Again, if the quality of the resource-holding male is positively correlated with resource value, and judging resource value is more difficult than assessing male quality (Waage 1984), females could indirectly acquire high-quality mates by examining resources (e.g. Fincke 1992). Passive female mate choice (Thornhill and Alcock 1983) should provide numerous advantages to females (e.g. avoid the costs of inter-sexual contact such as energy expenditure, physical injury and parasite and disease transmission) if resource value is a reliable predictor of male genetic quality.

Fifth, females could choose a breeding situation based on some combination of male phenotype and resource value (e.g. birds, Yasukawa 1981; fish, Thompson 1986; mammals, Balmford et al. 1992; crustaceans, Backwell and Passmore 1996; insects, Jennions 1998), perhaps by using a threshold-criterion tactic of choice (Wittenberger 1983). This would involve selectively weighting the quality of both the male and the resource and then combining them into a single index of suitability. Alternatively, females could use a two-step process whereby all males are assessed based on one component and then a subset of those are judged on the second component (Thornhill 1983; Backwell and Passmore 1996). In either case, females should give priority to resource quality because of their immediate benefits (Møller and Jennions 2001a); hence, females should mate with the first male encountered who meets her minimum criteria (Wittenberger 1983).

The final hypothesis is the null model of random female settlement (Wootton et al. 1986) or neutral-mate-choice (Lightbody and Weatherhead 1988). Although the neutral-mate-choice hypothesis is a null model and female choice is random, it is not a 'truly' null model because neutral choice predicts female behaviour to be optimal with respect to maximizing fitness whereas a true null model of random choice predicts that female settlement is not optimal (Lightbody and Weatherhead 1988). Both models predict that males with larger territories acquire more female mates (i.e. harem size correlates positively with territory/resource area) (Lightbody and Weatherhead 1988).

If females preferentially settle on the best available resources and males with greater RHP control these resources, then a strong positive relationship between male RHP, resource quality and male mating success is predicted, perhaps even reaching $r = 1.0$ if rank-based methods are used (e.g. Spearman rank or Kendall tau correlation). Due to measurement error and biological noise, perfect correlations ($r = 1.0$) are, however, rare in biology even for well-established relationships (Jennions et al. 2001; Møller and Jennions 2002). Moreover, the inaccurate identification of either the male trait(s) important to RHP or the resource

characteristic sought by females will weaken the observed strength of the relationships.

If sexually receptive females are more strongly attracted to higher-quality resources and males with greater RHP

monopolize these resources (Fig. 1 Scenario 1a and b), then males with larger RHP should have greater reproductive success (Fig. 1 Scenario 1c). Many studies have investigated this hypothesis by determining whether dominant males

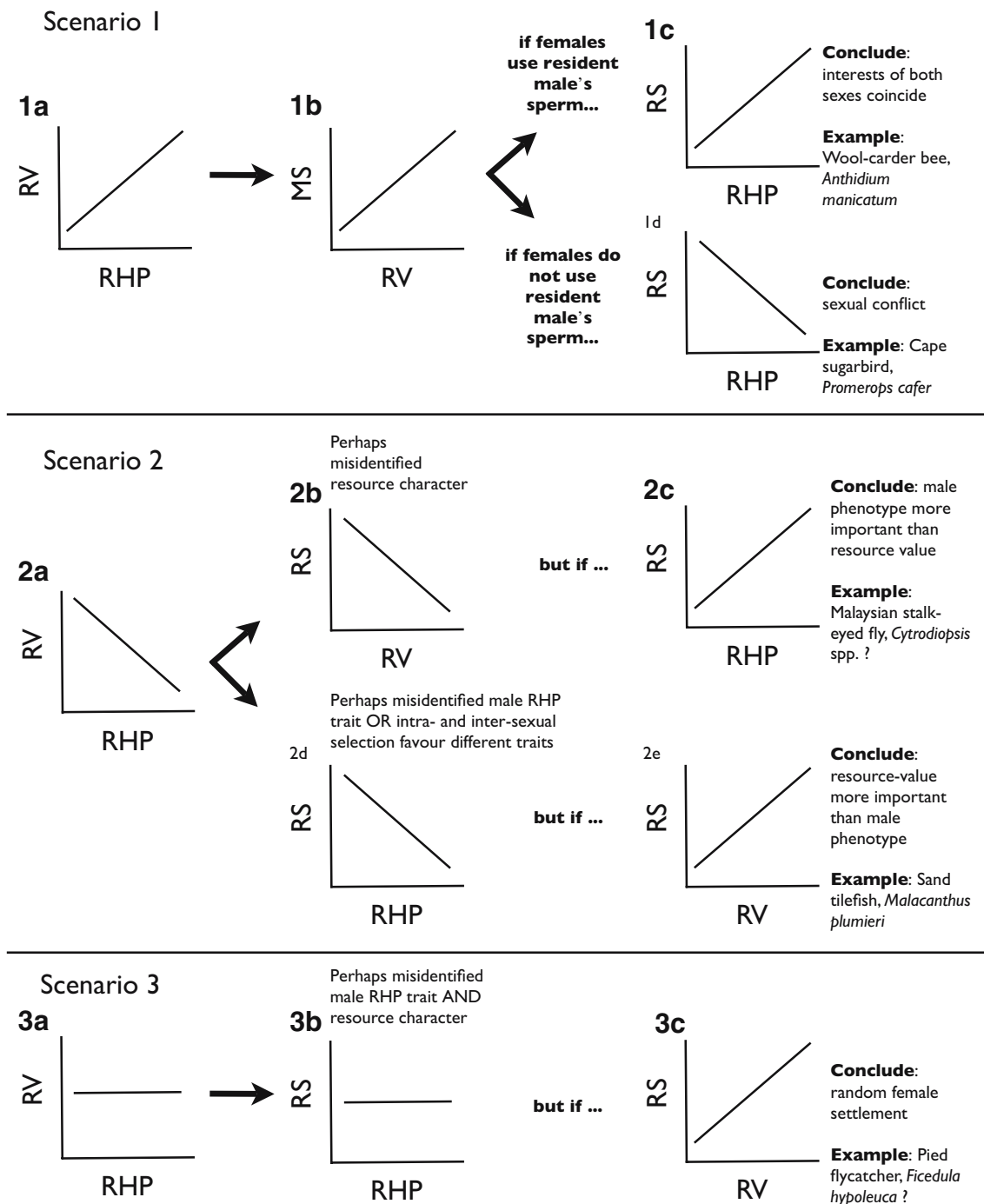


Fig. 1 The importance of testing each relationship among resource-value (RV), male resource-holding potential (RHP) as well as male reproductive (RS) and reproductive (RS) success within a species. Each scenario presents the possible mechanisms driving either a positive (Scenario 1), negative (Scenario 2) or no (Scenario 3) correlation between RV vs. RHP. Alternative hypotheses for a given relationship are presented above figures. For example, if a positive correlation is found between RV

vs. RHP (*Scenario 1a*), does this mean that males with greater RHP have greater RS because they own sites having greater RV (*Scenario 1c*)? No, because although more females may visit (and potentially mate) at sites having greater RV (*Scenario 1b*), females may prefer to use the sperm of males with lower RHP (*Scenario 1d*). This would arise if, perhaps, there were a trade-off among male traits selected by male-male competition versus female mate choice

(i.e. those whose RHP is inferred to be greater) have increased reproductive success (e.g. Gwynne and Jamieson 1998; Kelly 2005). This is problematic because a correlative estimate of a single relationship cannot reveal the underlying mechanisms driving male reproductive success (Fiske et al. 1998). In many cases (e.g. Kelly 2005), concluding that males with large RHP also have higher reproductive success implicitly assumes that the first two statements are correct (i.e. RHP vs. RV and RV vs. MS) (Fig. 1 Scenario 1a – b) and also assumes that mating success equals reproductive success (Brown et al. 1997). That mating success equals reproductive success is a safe assumption (e.g. Côte and Hunte 1989); however, if intense sexual conflict arises and females prefer to use the sperm of males with traits unrelated to RHP then resource-defence should breakdown (Fig. 1 Scenario 1d) (Brown et al. 1997; Arnqvist and Rowe 2005).

Quantifying the strength of one relationship and assuming the other two to be correct does not test all relationships directly and therefore cannot be used to infer that males with greater RHP hold better resources or that better resources attract more females. In other words, correlating a single factor (e.g. male RHP) with mating or reproductive success only explains part of the puzzle of what attracts females to certain locations and why particular males reside at those locations. For example, a negative relationship between RV and male RHP from an observational field study (e.g. Baird 1988), can be caused by a number of factors (Fig. 1 Scenario 2): perhaps there is a stronger female preference for either the resource or male phenotype, trade-offs might exist because male traits that increase success during male combat decrease male attractiveness to mate choosing females, or perhaps the relationship is a product of either a misidentified resource-character or male RHP trait. By further investigating each of the other two relationships (RS vs. RV and RS vs. RHP; Fig. 1 Scenario 2b–e) investigators can gain a better understanding of why males with larger RHP apparently hold poorer resources. For example, if resource-value is negatively correlated with reproductive success (Fig. 1 Scenario 2b) but male RHP is positively correlated with reproductive success (Fig. 1 Scenario 2c), then female mate choice is likely based more on male phenotype than resource value.

Random female settlement would be indicated by a positive relationship between RV (i.e. territory area) vs. RS (Fig. 1 Scenario 3c) and no relationship between RV vs. male RHP (Fig. 1 Scenario 3a) and between RS vs. male RHP (Fig. 1 Scenario 3b). Alternatively, the lack of relationship in Scenarios 3a and b could be due to misidentified traits or resource characters.

A central prediction of behavioural ecology is that male RHP, resource quality and male reproductive success are all positively correlated (Emlen and Oring 1977; Andersson

1994; Brown et al. 1997; Shuster and Wade 2003). Although many studies have supported this prediction, other studies suggest that mating with a more dominant male may be costly to females. For example, strong negative relationships have been reported between male RHP and resource-value (e.g. Baird 1988), reproductive success and resource-value (e.g. Villalobos and Shelly 1991; Oliveira et al. 2000) and reproductive success and male RHP (e.g. Savalli 1994a). It is clear that individual studies inadequately describe general patterns in nature. Here, I use meta-analysis to quantitatively describe the general pattern of these relationships in animals. Although others have qualitatively assessed the relationships between male RHP, resource value and male reproductive success in resource-defence animals (e.g. Baker 1983; Fitzpatrick and Wellington 1983; Thornhill and Alcock 1983; Maher and Lott 2000), that approach does not measure the magnitude of the effect size nor does it give any indication as to the sources of variation in effect sizes. I predict that the relationships between male RHP, resource-value and reproductive success should be significantly positive. In other words, I expect that male RHP and resource-value should explain a large amount of the variation in male reproductive success. Additionally, I predict that male RHP and resource value will explain more of the variation in male reproductive success when examined experimentally, rather than by observational studies, because variation due to confounding variables will be eliminated in this type of study. Finally, I also investigated whether effect sizes for the different relationships vary among taxa and whether certain male traits representing RHP have a stronger effect on resource-value and reproductive success than other traits.

Materials and methods

Data sets

I searched the literature by entering the terms ‘resource defence’, ‘resource defense’, ‘territoriality’, ‘territory’ and ‘territorial’ into Web of Science (ISI). I looked for studies reporting information on the relationship between (1) male reproductive success and defended resource-value, (2) male reproductive success and male resource-holding potential and/or (3) resource-value and male resource-holding potential. I make no claim to have included all relevant studies but there is no immediately obvious reason why this search strategy would not yield a representative sample of published studies.

The original authors reported a large number of metrics for male reproductive success and included: the number of females that either copulated, laid eggs, visited a resource patch or associated with a male for a period of time (i.e. harem size); number of offspring hatched, fledged or reared

to maturity; and pair-bond duration. Resource-value was typically measured as the quantity of some material required by females (e.g. number of flowers, biomass of edible vegetation, proximity to water, degree of predation risk, nest size). In some cases, investigators used male ‘ownership’ of a resource patch or territory as a metric of resource-value – patches controlled by males were considered to be high-value sites. Male resource-holding potential was defined based on weapon size (e.g. mandible, horn or antler length), body size (e.g. weight, wing, tarsus, pronotum or elytra length), body condition, age, traits that signal fighting ability (e.g. colour patches or song characteristics) and ‘other’ traits (e.g. experience, residency, date of arrival on a territory). All definitions are those of the original authors: whether the definitions of the original authors are appropriate is not the focus of this paper. The important point to note is that these are how the terms have been defined and used in the literature.

Each study was classified as to whether its methodological approach was experimental or observational. Experimental studies involved manipulating either the trait putatively responsible for defining male RHP and/or the resource character sought by females as well as controlling possible confounding variables (e.g. temperature, light cycle, mating history etc). Most studies were unambiguously classified; however, some studies did not fit the experimental definition. These studies were classified as experimental on the grounds that the investigator manipulated some aspect of the study and so the study was not based on a random set of observations. For example, Wells (1977) observed a sample of frogs that he collected and introduced into an enclosed pond; I classified this as ‘experimental’.

Meta-analysis

I retrieved data from the text or tables or indirectly by measuring figures for each study. I calculated effect sizes as Pearson product-moment correlation coefficients (Hedges and Olkin 1985; Rosenthal 1991; Cooper and Hedges 1994) and transformed data to r using the *MetaWin* software package (Rosenberg et al. 2000) if presented in another form (e.g. t , F , χ^2 , Mann-Whitney U). When the means and standard deviations were available I calculated the effect size estimate Hedge’s g , which was then transformed to r .

I followed the protocol used by others (e.g. Jennions et al. 2001; Møller and Jennions 2001a; Torres-Vila and Jennions 2005) and only briefly describe the methodology here. First, correlation coefficients were z -transformed and weighted by their sample size. A sample was defined as a single test for an effect.

Samples within studies and multiple studies of a single species lack statistical independence (Thornhill and Møller

1998); therefore, I examined results at the level of samples, studies and species. If qualitatively similar conclusions are reached at all three levels of analysis it is reasonable to assume that the level of analysis is relatively unimportant. The transformed coefficients were combined for each level of analysis and weighted by average sample size per sample within studies or studies within species.

When examining the effect of moderator variables (e.g. male RHP trait-type, resource character, taxon or methodology), I used a single effect for each species for each moderator variable of interest in order to maintain statistical independence. For example, the resource-holding potential of male pheasants, *Phasianus colchicus*, is influenced by weapons (spurs), body size, signals and age and multiple effect sizes have been calculated for some of these traits. Consequently, a single mean effect size was calculated for each trait for this species and these values were then used in the meta-analysis. There were too few species having both experimental and observational effect sizes available and so could not make paired comparisons (cf. Torres-Vila and Jennions 2005).

Effect sizes were calculated using the mixed-effects model which allows a true random component, in addition to sampling error, as a source of variation in effect size among studies (Hedges and Olkin 1985). The null hypothesis for each analysis was that effect size equalled zero. I tested this hypothesis by examining the 95% confidence intervals for the mean weighted effect size; overlap with zero would support the null hypothesis at the 0.05 α -level. *MetaWin* provides mean effect size and 95% confidence intervals calculated using a bias-corrected bootstrap approach (999 replicates). Similarly, I examined confidence intervals to see if the mean effect size differed significantly from 1.0. I also report the within-group heterogeneity (Q_w) for each group of studies, assuming Q follows a χ^2 distribution with $df = \text{number of studies} - 1$. Mean weighted effect sizes (Z_r) were back-converted and are expressed in terms of r .

I tested whether the mean effect size differed between groups (e.g. among taxa) by testing for significant between-group heterogeneity (Q_b) using randomisation tests based on 1,000 replicates. Within-group heterogeneity (Q_w) was calculated for groups with $n_e > 5$. If there is no data structure incorporated into the summary analysis (i.e. no moderator variables) then total heterogeneity is calculated (Q_T) (Rosenberg et al. 2000). I tested whether the magnitude and direction of mean effect sizes are consistent among the three relationships (RHP vs. RV, RHP vs. RS and RV vs. RS) using a subset of species ($n = 22$) in which all three relationships of interest have been reported in the literature. By focusing on this subset of data I control for the effect of species because in the original analysis different species contribute to each of the three relationships and this could, therefore, bias the overall analysis and

subsequent interpretation. For each species there was a single effect for each relationship. Consequently, I analyzed these data using Cohen's q by calculating the difference in mean effect size per relationship and then testing whether it differs significantly from zero (Rosenthal 1994).

I calculated Rosenthal's fail-safe number for groups with $n_e > 5$ to assess the robustness of my results. This estimates the number of studies with no effect that are required to nullify an observed statistically significant effect size at $\alpha = 0.05$ (Rosenthal 1991). By convention, a conclusion is generally considered robust if the fail-safe number exceeds $5n_e + 10$, where n_e is the reported number of analysis units (i.e. samples, studies or species).

The estimate of a mean weighted effect size could be inaccurate if a publication bias exists (Rosenthal 1991; Begg 1994). This phenomenon has been much debated among meta-analysts (e.g. Rosenthal 1991; Begg 1994; Duval and Tweedie 2000a; Duval and Tweedie 2000b), including evolutionary ecologists (e.g. Arnqvist and Wooster 1995; Palmer 1999; Jennions and Møller 2002; Kotiaho and Tomkins 2002; Koricheva 2003; Jennions et al. 2004; Tomkins and Kotiaho 2004; Møller et al. 2005). The only direct method to address this problem is to compare published and unpublished studies. Several recent studies (Møller and Thornhill 1998; Jennions et al. 2001; Møller and Jennions 2001a; Koricheva 2003; Møller et al. 2005) have done this and, in each case, the effect sizes of the two categories of studies did not differ. I did not have access to unpublished data so I used two indirect methods to address this issue.

First, I calculated the Begg-Mazumdar correlation between standardized effect size and study sample size (r -bias). This statistic should be interpreted with caution, however, because it has low statistical power with sample sizes (n_e) fewer than 25 (Møller and Jennions 2001b).

Second, I used the iterative 'trim and fill' method of Duval and Tweedie (2000a, b) to estimate the number of 'missing' studies based on a funnel plot of the data (i.e. effect size vs. sample size) and then calculated the mean effect if these hypothetical 'missing' studies are included. This procedure is based on two assumptions: there should be a symmetric distribution of observed effect sizes around the 'true' effect size if publication bias is absent and the most extreme results, typically those with low sample size and high variance, have not been published.

Third, I tested whether there was a correlation between date of publication and effect size.

Results

As species are the focus of this review and all three levels of analysis (i.e. samples, studies and species) gave similar

results, I present and discuss only those findings from the species-level of analysis. The results from the sample- and study-levels of analysis, as well as raw data, are provided as Electronic Supplemental Material (S1 to S4).

Male resource-holding potential vs. resource-value

For the 53 species (from $n = 63$ studies), the weighted average effect size of $r = 0.37$ was significantly greater than zero and the variation in effect size was no more than expected due to sampling error (Table 1). There was no evidence of publication bias (Table 1; Fig. 2a) and the addition of one putative missing study resulted in a slightly reduced corrected mean effect size of $r = 0.35$ (95% C.I.: 0.27 – 0.43). The mean effect size for experimental studies ($r = 0.51$, 95% CI: 0.35 – 0.68) was larger than for observational studies ($r = 0.35$, 95% CI: 0.24 – 0.44) but the difference was not significant ($Q_b = 2.44$, $df = 1$, $P = 0.14$). For each of the six types of male traits used as indices of RHP, individuals with larger values controlled resources of greater value (Table 1). The strength of these relationships was remarkably consistent for the different types of traits ($Q_b = 0.58$, $df = 5$, $P = 0.99$). An analysis by taxon (each species contributing one effect size) showed that mean weighted effect size was significantly greater than zero for all taxa but fish (Table 1). There was also no difference in effect sizes among taxa ($Q_b = 0.96$, $df = 2$, $P = 0.59$; only tested using taxa with $n_e > 5$ species).

Resource-value vs. male reproductive success

The weighted average effect size for the 40 species of $r = 0.45$ (from $n = 45$ studies) was significantly greater than zero but the among-effect size variation was statistically significant (Table 2). This significant heterogeneity was caused by a single large effect size for the walnut fly *Rhagoletis boycei* ($r = 0.99$; Papaj 1994). Its removal considerably lowered the observed heterogeneity ($Q_w = 51.2$, $df = 38$, $P = 0.05$) but did not change the original conclusion (recalculated $r = 0.41$, 95% CI: 0.32–0.51, $n = 39$). Partial correlations were performed for three species with a mean effect size of $r = 0.17$ (95% CI: 0.05 – 0.30). A trim and fill analysis suggested that six studies were missing (see also Fig. 2b) and the corrected mean effect size of $r = 0.34$ (95% CI: 0.27 – 0.41) was smaller but still significantly greater than zero. The mean effect sizes for observational ($r = 0.45$, 95% CI: 0.31 – 0.59) and experimental studies ($r = 0.44$, 95% CI: 0.25 – 0.61) did not differ significantly ($Q_b = 0.004$, $df = 1$, $P = 0.95$). The significant variation in effect size was not explained by differences between estimates based on the two main categories of resource value (quality or size) ($Q_b = 0.10$, $df = 1$, $P = 0.81$). Mean effect sizes for estimates based on territory quality, size and ownership

Table 1 Summary of mean effect sizes (Pearson's r with 95% bias-corrected bootstrapped confidence intervals) for the relationship between resource-holding potential (RHP) and resource-value (RV) at the species level of analysis

| | Effect size | | | Effect size heterogeneity ^a | | | Fail-safe no. | r -bias |
|----------------|-------------|------|------------|--|------|------|------------------|-----------|
| | n_e | r | 95% CI | Q_w | df | P | | |
| All species | 53 | 0.37 | 0.28–0.46 | 49.2 ^b | 52 | 0.58 | 933 ^c | -0.20 |
| Weapon | 7 | 0.29 | 0.17–0.40 | 5.2 | 6 | 0.51 | 39 | 0.0 |
| Signal | 13 | 0.31 | 0.22–0.43 | 11.8 | 12 | 0.46 | 126 ^c | 0.0 |
| Age | 5 | 0.38 | 0.03–0.70 | 2.7 | 4 | 0.61 | 0 | -0.1 |
| Body size | 38 | 0.37 | 0.25–0.47 | 35.2 | 37 | 0.55 | 423 ^c | -0.25 |
| Body condition | 8 | 0.39 | 0.26–0.55 | 6.4 | 7 | 0.49 | 45 | -0.36 |
| Other | 5 | 0.33 | 0.08–0.57 | 4.5 | 4 | 0.35 | 3 | -0.21 |
| Insect | 25 | 0.36 | 0.24–0.47 | 19.1 | 24 | 0.75 | 191 ^c | -0.27 |
| Bird | 10 | 0.41 | 0.22–0.58 | 9.5 | 9 | 0.39 | 36 | -0.07 |
| Fish | 8 | 0.23 | -0.12–0.47 | 5.5 | 7 | 0.59 | 0 | -0.48 |
| Mammal | 3 | 0.22 | 0.19–0.24 | – | – | – | – | – |
| Crustacean | 2 | 0.14 | 0.04–0.24 | – | – | – | – | – |
| Amphibian | 4 | 0.68 | 0.50–0.86 | – | – | – | – | – |
| Reptile | 1 | 0.80 | – | – | – | – | – | – |

Data were grouped on the basis of RHP trait (e.g. weapon, signal etc.) and higher taxa (e.g. insect, bird etc.). Within-group heterogeneity in effect sizes (Q_w), Rosenthal's fail-safe number, the Begg–Mazumdar correlation between standardized effect size and sample size (r -bias) and the number of effect sizes (n_e) are provided

^a Does not include taxa with $n_e < 5$

^b Q_T because no data structure

^c Rosenthal's fail-safe number greater than $5n_e + 10$

were all significantly greater than zero, but only those for resource quality exhibited significantly greater variation than expected due to sampling error (Table 2).

Males holding higher quality resources had significantly greater reproductive success in all major taxa except Crustacea (Table 2). There was no significant difference in the mean effect size among taxa with $n_e > 5$ ($Q_b = 0.66$, $df = 2$, $P = 0.85$). There was high heterogeneity within each taxa (Table 2) but this was due to a single outlier in each taxa. Removal of these outliers removed the observed heterogeneity within each taxon (Table 2).

Male resource-holding potential vs. male reproductive success

The weighted average effect size of $r = 0.37$ (from $n = 69$ studies) was significantly greater than zero and the variation among effect sizes was not statistically significant (Table 3). Partial correlations were performed for four species and the mean effect size was not significantly different from zero ($r = 0.31$, 95% CI: -0.14 – 0.63). There was no publication bias (Table 3; Fig. 2c). A “Trim and Fill” analysis suggested that there were 10 “missing” studies and their addition actually resulted in a larger corrected mean effect size of $r = 0.47$ (95% CI: 0.37 – 0.55). The mean effect size for experimental studies ($r = 0.63$, 95% CI: 0.30 – 0.88) was significantly greater than that for observational studies ($r = 0.34$, 95% CI: 0.24 – 0.43; $Q_b = 6.83$, $df = 1$, $P = 0.009$). The type of male trait used to estimate RHP did not

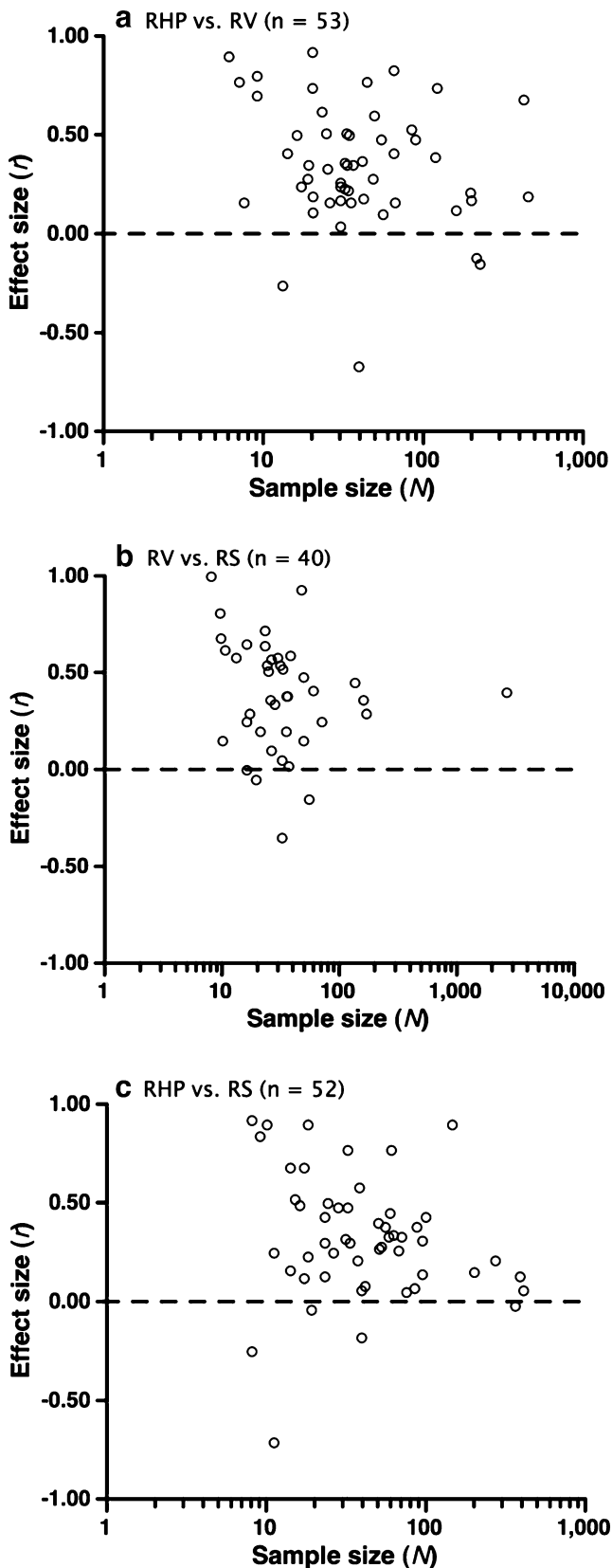
explain a significant amount of variation in effect sizes ($Q_b = 2.4$, $df = 4$, $P = 0.66$; only traits with $n_e > 5$). When analysed by trait type, only those categorized as ‘other’ has a statistically non-significant mean effect size (Table 3). Similarly, taxon did not explain a significant amount of variation in effect sizes ($Q_b = 1.03$, $df = 2$, $P = 0.60$; only taxa with $n_e > 5$).

Comparison of species-level effect sizes

In line with the predictions of Scenario 1 (Fig. 1) there was no difference among mean global effect sizes calculated for each of the three relationships (RHP vs. RV: $r = 0.37$, RV vs. RS: $r = 0.45$ and RHP vs. RS: $r = 0.37$; $Q_b = 1.8$, $df = 2$, $P = 0.47$).

Effect sizes for all three relationships were available for 22 species (Table 4; Fig. 3). An analysis of this subset again supports the predictions of Scenario 1 (Fig. 1) because the mean effect size did not differ among the three relationships (RHP vs. RS - RV vs. RS, Cohen's $q = 0.012$, 95% CI: -0.13 – 0.15; RHP vs. RS - RHP vs. RV, $q = 0.11$, -0.04 – 0.25; RV vs. RS - RHP vs. RV, $q = 0.11$, -0.03 – 0.26). However, inspection of an interaction plot (Fig. 3) suggests an interaction between species and relationship-type; suggesting that Scenarios 2 and 3 (Fig. 1) can better explain the interrelationships within some species than Scenario 1.

The three relationships also did not differ when considering only effect sizes from experimental studies (RHP vs. RS - RV vs. RS, Cohen's $q = 0.28$, 95% CI: -0.58 –



◀ **Fig. 2** The relationship between study sample size (N) and effect size (r) at the species-level of analysis for the relationship between **a** resource-holding potential (RHP) and resource-value (RV), **b** resource-value (RV) and male reproductive success (RS) and **c** resource-holding potential (RHP) and male reproductive success (RS). The dashed line represents an effect size of zero and the solid line is for the observed weighted mean effect size

0.96; RHP vs. RS – RHP vs. RV, $q = 0.18, -0.54 - 0.77$; RV vs. RS – RHP vs. RV, $q = 0.10, -0.58 - 0.29$.

Discussion

A long-standing hypothesis in behavioural ecology posits that males with greater resource-holding potential control resource sites or territories deemed more valuable by sexually-receptive females and, thereby, males controlling such sites accrue greater reproductive success (Emlen and Oring 1977; Andersson 1994; Brown et al. 1997; Shuster and Wade 2003) (see Fig. 1 Scenario 1a-c). This hypothesis has historically been investigated using three separate but non-mutually exclusive relationships (RHP vs. RV, RV vs. RS and RHP vs. RS). My meta-analysis supports the aforementioned hypothesis on four grounds. First, the global mean effect size for each relationship at the species-level (observational and experimental studies combined) were of similar magnitude ($r = 0.37, 0.45$ and 0.37) and all significantly greater than zero. Second, these global effect sizes were not spurious as experimental studies showed a significant positive effect of male RHP and RV on male reproductive success. However, in only one case (RHP vs. RS) did the mean effect size based on experiments significantly outweigh the mean effect based on observations. Third, partial correlations showed that males with greater RHP had higher reproductive success while statistically controlling for resource-value and males controlling better resources had greater reproductive success while statistically controlling for male RHP. Finally, an analysis of a subset of 22 species for which all relationships have been quantified showed that all three effect sizes were of similar magnitude and, on average, significantly positive.

The interaction plot suggests that the magnitude and sign of a particular relationship can differ widely among species (Fig. 3). For example, male sand tilefish, *Malacanthus plumieri*, with greater RHP do not hold better resources nor do they gain greater reproductive success; however, sites of greater resource-value host males with higher reproductive success (see Fig. 1 Scenarios 2a, d and e). This result suggests that either resource-value is more important to female sand tilefish than male phenotype or perhaps, more importantly, researchers have incorrectly identified the traits determining RHP (see below). In contrast, male yellow-shouldered widowbirds, *Euplectes macrourus*, with greater

Table 2 Summary statistics for the relationship between resource-value (RV) and reproductive success (RS) at the species level of analysis

| | Effect size | | | Effect size heterogeneity ^a | | | Fail safe no. | <i>r</i> -bias |
|-------------|----------------------|----------|------------|--|-----------|---------------------|-------------------|----------------|
| | <i>n_e</i> | <i>r</i> | 95% CI | <i>Q_w</i> | <i>df</i> | <i>P</i> | | |
| All species | 40 | 0.45 | 0.34–0.55 | 79.6 ^b | 39 | <0.001 | 1104 ^c | –0.27 |
| Quality | 29 | 0.42 | 0.30–0.55 | 75.1 | 28 | <0.001 | 712 ^c | –0.36 |
| Size | 19 | 0.39 | 0.17–0.58 | 15.1 | 18 | 0.66 | 49 | –0.08 |
| Ownership | 2 | 0.31 | 0.25–0.35 | – | – | – | – | – |
| Insect | 14 | 0.50 | 0.36–0.69 | 51.6 | 13 | <0.001 ^d | 287 ^c | –0.39 |
| Bird | 10 | 0.44 | 0.20–0.68 | 84.8 | 9 | <0.001 ^e | 234 ^c | –0.15 |
| Fish | 7 | 0.41 | 0.19–0.60 | 12.8 | 6 | 0.03 ^f | 42 | –0.14 |
| Mammal | 4 | 0.38 | 0.20–0.57 | – | – | – | – | – |
| Crustacean | 2 | 0.006 | –0.15–0.25 | – | – | – | – | – |
| Amphibian | 2 | 0.58 | 0.51–0.64 | – | – | – | – | – |
| Reptile | 1 | 0.68 | – | – | – | – | – | – |

See Table 1 for description of column headings

^a Does not include taxa with $n_e < 5$

^b Q_T because no data structure

^c Rosenthal's fail-safe number greater than $5n_e + 10$

^d Removal of outlier ($r = 0.99$, *Rhagoletis boycei*): $Q_w = 14.4$, $df = 12$, $P = 0.28$

^e Removal of outlier ($r = -0.05$, *Euplectes macrourus*): $Q_w = 6.1$, $df = 8$, $P = 0.63$

^f Removal of outlier ($r = 0.05$, *Pomatoschistus minutus*): $Q_w = 3.6$, $df = 4$, $P = 0.46$

RHP have greater reproductive success. It appears though that higher-RHP males do not necessarily hold better territories nor do more-valuable territories increase male mating success (Savalli 1994a, b). Thus, female *E. macrourus* may choose male phenotype over resource characteristics. Alternatively, the resource characteristic sought by females in this species may have been inaccurately identified by the investigators (see below). Unfortu-

nately, few of the effect sizes listed for the subset of 22 species were acquired experimentally (Table 4). By increasing our use of an experimental approach in investigations of resource-defence species we will not only more accurately identify what phenotypic traits and resource characteristics are important to male reproductive success but also better estimate the size of the effect these traits and characters have on male fitness (see also Candolin 2003).

Table 3 Summary statistics for the relationship between resource-holding potential (RHP) and reproductive success (RS) at the species level of analysis

| | Effect size | | | Effect size heterogeneity ^a | | | Fail-safe no. | <i>r</i> -bias |
|----------------|----------------------|----------|------------|--|-----------|----------|------------------|--------------------|
| | <i>n_e</i> | <i>r</i> | 95% CI | <i>Q_w</i> | <i>df</i> | <i>P</i> | | |
| All species | 52 | 0.37 | 0.27–0.46 | 60.2 ^b | 51 | 0.18 | 951 ^c | –0.26 |
| Weapon | 5 | 0.32 | 0.28–0.35 | 0.62 | 4 | 0.96 | 57 ^c | –0.20 |
| Signal | 21 | 0.43 | 0.28–0.58 | 25.1 | 20 | 0.20 | 159 ^c | –0.003 |
| Age | 8 | 0.24 | 0.05–0.42 | 4.7 | 7 | 0.69 | 3 | –0.18 |
| Body size | 38 | 0.30 | 0.19–0.41 | 35.9 | 37 | 0.52 | 296 ^c | –0.28 |
| Body condition | 4 | 0.49 | 0.14–0.79 | – | – | – | – | – |
| Other | 5 | 0.33 | –0.08–0.59 | 3.8 | 4 | 0.44 | 0 | 0.60 |
| Insect | 25 | 0.39 | 0.25–0.54 | 31.2 | 24 | 0.15 | 190 ^c | –0.48 [*] |
| Bird | 12 | 0.27 | 0.10–0.42 | 8.5 | 11 | 0.67 | 16 | 0.48 |
| Fish | 7 | 0.42 | 0.14–0.65 | 6.1 | 6 | 0.41 | 12 | –0.64 |
| Mammal | 3 | 0.64 | 0.43–0.77 | – | – | – | – | – |
| Crustacean | 2 | 0.10 | 0.06–0.16 | – | – | – | – | – |
| Amphibian | 3 | 0.32 | 0.14–0.43 | – | – | – | – | – |

See Table 1 for description of column headings

^a Does not include taxa with $n_e < 5$

^b Q_T because no data structure

^c Rosenthal's fail-safe number greater than $5n_e + 10$

^{*} $P < 0.05$

Table 4 Effect sizes (r) for each of three relationships for the subset of species in which all three relationships have been investigated

| Species | Taxon | RHP vs. RV | RHP vs. RS | RV vs. RS |
|---|-----------|--------------------|---------------------|--------------------|
| <i>Acrocephalus arundinaceus</i> | Bird | 0.374 | 0.302 | 0.340 ^c |
| <i>Anthidium manicatum</i> ^a | Insect | 0.350 | 0.314 | 0.290 |
| <i>Anthidium palliventre</i> ^a | Insect | 0.170 | 0.251 | 0.095 |
| <i>Anthidium porterae</i> ^a | Insect | 0.483 | 0.486 | 0.002 |
| <i>Bothus poda</i> ^a | Fish | 0.700 | 0.840 | 0.148 |
| <i>Euplectes macrourus</i> ^a | Bird | 0.115 ^c | -0.044 ^c | -0.054 |
| <i>Ficedula hypoleuca</i> | Bird | 0.158 ^c | 0.078 ^c | 0.543 |
| <i>Hemideina crassidens</i> ^a | Insect | 0.500 ^c | 0.344 ^c | 0.655 ^c |
| <i>Kobus vardonii</i> ^a | Mammal | 0.243 | 0.681 | 0.291 |
| <i>Malacanthus plumieri</i> ^a | Fish | -0.671 | -0.180 | 0.580 |
| <i>Megaloprepus coerulatus</i> ^a | Insect | 0.528 | 0.173 | 0.384 |
| <i>Nannophya pygmaea</i> ^a | Insects | -0.262 | 0.517 | 0.589 |
| <i>Neacoryphus bicrucis</i> | Insect | 0.116 | 0.382 | 0.814 |
| <i>Notobitus meleagris</i> ^a | Insect | 0.257 | 0.480 | 0.379 |
| <i>Ophioblennius atlanticus</i> ^a | Fish | 0.222 | 0.578 | 0.202 |
| <i>Phasianus colchicus</i> ^a | Bird | 0.156 ^c | 0.302 | 0.720 |
| <i>Pomatoschistus minutus</i> | Fish | 0.506 ^c | 0.485 ^c | 0.053 |
| <i>Promerops cafer</i> ^a | Bird | 0.160 | -0.254 | 0.617 |
| <i>Rana catesbeiana</i> ^a | Amphibian | 0.509 | 0.400 | 0.514 |
| <i>Rana clamitans</i> ^a | Amphibian | 0.625 ^c | 0.430 ^c | 0.638 ^c |
| <i>Troglodytes troglodytes</i> ^a | Bird | 0.330 | 0.497 ^c | 0.540 |
| <i>Parablennius sanguinolentus parvicornis</i> ^a | Fish | 0.437 | 0.678 | -0.35 |

^a All three relationships reported from single study (i.e. same date and location but not necessarily same publication)

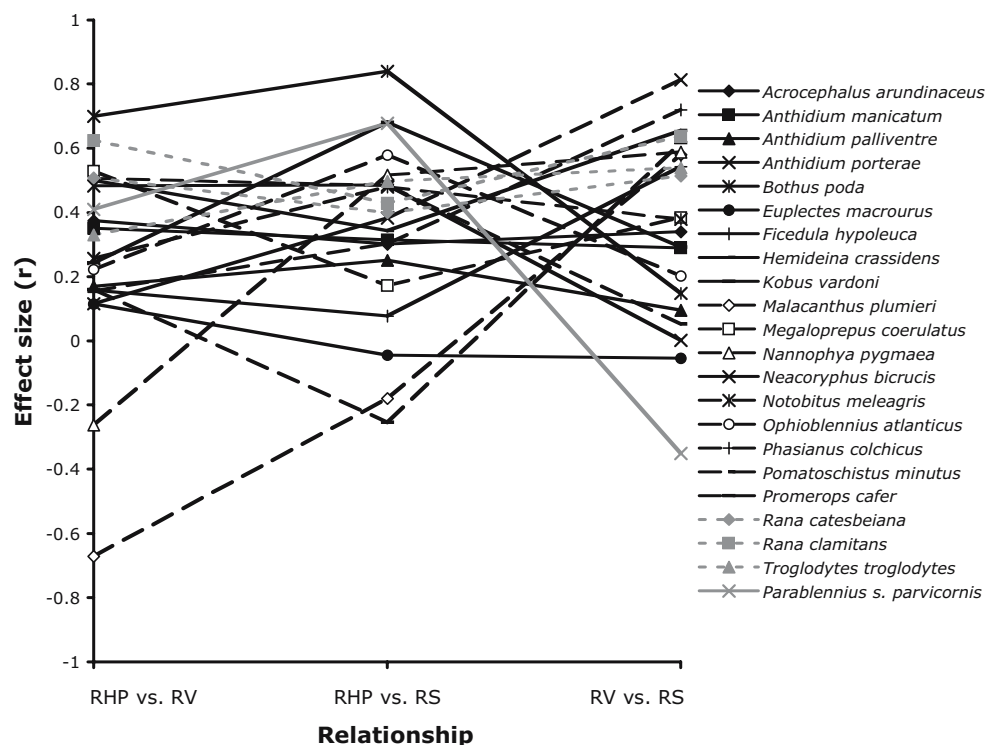
^c Experimental effect size contributed to overall mean effect size

Trait identification and explained variation

The mean species-level effect sizes reported here were about twice as large as those typically reported for

evolutionary ecological studies ($r = 0.18 - 0.193$, Møller and Jennions 2002). Although the mean effect size for RHP vs. RV and RHP vs. RS were both $r = 0.37$, male RHP traits only account for 14% of variation among males in the

Fig. 3 An interaction plot of effect size (r) for the relationship between 1) male resource holding potential and resource value, 2) male resource holding potential and reproductive success and 3) resource value and reproductive success for each 22 species. See Table 4 for the taxa to which each species belongs



quality of the resource held and the reproductive success they acquired. The amount of explained variation was only marginally greater for RV vs. RS at 20%. Thus, in order to detect a significant relationship in a single study between, for example male RHP and resource-value at the 0.05 α -level with 80% power, a minimum sample size of 52 is required. Such a sample size is larger than those typically used to investigate this relationship (Electronic Supplemental Material S2).

Contrary to prediction, only RHP vs. RS displayed a significantly larger average effect size for experimental studies compared with observational ones. This result is most likely due to our greater ability to identify and experimentally manipulate male traits that signal RHP compared with those representing resource quality; particularly, if resource quality is determined by something difficult to quantify, such as the greenness of the grass in a patch, for example. Alternatively, perhaps male RHP simply has a stronger effect on male reproductive success than resource quality. Perhaps our ability to identify, and then experimentally manipulate, resource quality will improve as our methods and techniques improve. For example, investigators are now able to, with relative ease, biochemically assay the nutritional quality of ingested materials (Heimpel et al. 2004), conduct remote video surveillance (Stewart et al. 1997) as well as better follow the movements of very small animals (e.g. crickets and dragonflies) with radiotelemetric devices (Lorch and Gwynne 2000). Consequently, our ability to unlock many of the secrets of an animal's life is continually improving and with that our ability to experimentally manipulate factors putatively important to male fitness.

Both the identity of the species used and the number of taxa upon which each effect size is based differed for each relationship. This could be a problem if, for example, insects tend to have a stronger relationship for RHP vs. RS and are over-represented in estimates of this particular relationship. Insects and birds dominated each of three relationships examined in this meta-analysis. For example, insects account for 47%, 48% and 37% of the species in the calculation of RHP vs. RV, RHP vs. RS and RV vs. RS, respectively. Fewer studies were available for mammals, fish, crustaceans, amphibians or reptiles.

That the mean effect sizes reported here were all relatively larger than those typically found in evolutionary ecological studies and significantly positive is partly due to researchers having selected *a priori* species that they believed to have a resource-defence based mating system. In other words, studies are typically conducted on species in which we know males defend resources etc. so a positive effect should come as no surprise. This is not always the case, however. For example, Christy and Schober (1994) did not support their hypothesis of resource-defence in a

study on the fiddler crab *Uca beebei*. The paucity of published negative results at the sample- and study-level further supports the notion that investigators are not blindly testing whether an animal is territorial.

Four studies in my meta-analysis reported $r \sim 1.0$ (Hughes and Hughes 1985; Papaj 1994; Pryke and Andersson 2002; Pryke et al. 2002). Effect sizes of this magnitude are not the norm, particularly in field studies. Instead effect sizes, as evidenced in this meta-analysis, are often significantly greater than zero but far less than one because accurately identifying traits representing RHP or resource-value is difficult, measurement error is high and biological noise reduces the strength of the observed signal. I will address each factor below.

Investigators rarely know with high certainty which male trait(s) determine RHP or which characteristic defines the value of a territory for a given species, particularly when beginning research on a novel species. Instead, researchers typically correlate many traits putatively important to RHP with several different measures of territory quality or male reproductive success. Not surprisingly then, many traits turn out to be unimportant and consequently have a weak association with the type of resource held or with reproductive success. Because meta-analysis requires the inclusion of all relevant effect size estimates from each study, regardless of statistical significance, mean effect sizes tend to be underestimates. For example, although Pryke et al. (2002) reported a strong effect of collar colour (the determinant of male RHP) on territory size ($r \sim 1.0$, my calculation) in the red-collared widowbird, *Euplectes ardens*, the mean effect size for RHP vs. RV in this species was nearly halved at $r = 0.52$ because of the inclusion in their analysis of some unimportant traits such as tail asymmetry and culmen length (see Andersson et al. 2002). This begs the interesting question as to whether the traits identified *a posteriori* as being important would be so in a replicate study (see Kelly 2006a), or was it simply by chance that this particular trait came out strongly in a large correlation matrix?

The significant heterogeneity among effect sizes observed for RV vs. RS is also likely to reflect our inability to target the resource characteristic(s) important in determining its value to females. Our ability to identify important traits does not appear to have improved with time, as there was no relationship between publication date and effect size (as observed in other biological relationships). I note that an improvement over time in how accurately we identify important traits does not necessarily have to be confined to one's own study species – investigators can heed the lessons learnt by those investigating organisms with similar morphology and/or behaviour. For example, in the megachilid bee *Anthidium manicatum*, Severinghaus et al. (1981) tested and supported the hypothesis that male mating

success is dependent upon the number of flowers in a territory. This hypothesis was raised in an earlier study by Alcock et al. (1977) on the congeneric *A. maculosum*. Similarly effect size could increase with date of publication if investigators improve their knowledge of which resource/territory characteristics are important to females as well as increase their accuracy in measuring mating success (e.g. through video surveillance of resource sites).

One way to get around the problem of underestimating the effect of single traits is to adopt a multivariate approach (e.g. principal components analysis, PCA) thereby permitting the reduction of several important and related traits to a single variable. Such an approach would be particularly beneficial if several different trait types (e.g. behavioural and structural) worked in conjunction to establish RHP. No study reported in this meta-analysis used PCA to reduce different types of traits into one RHP variable. More common, but still found in only four studies (Lebas 2001; Andersson et al. 2002; Forstmeier 2002; Pryke and Andersson 2003a, b), was the use of PCA to distil several measures of one trait-type (e.g. structural) to a single variable representing, for example, body size (e.g. tarsus, culmen and wing length in the red-shouldered widowbird *Euplectes axillaris*, Pryke and Andersson 2003a, b).

Reducing several traits to a principal component would also be beneficial in situations where male-male competition and female mate choice operate differently upon a trait (s). For example, Moore (1990) showed that in *Libellula luctuosa* male-male competition selects directionally for larger body size while there is stabilizing intersexual selection for males of intermediate body size but with increased wing pigmentation. Therefore, in species where this type of situation seems likely to arise it would be prudent to measure several traits representing body size (e.g. thorax width, wing length) and traits known to influence female mate choice (e.g. area of wing pigmentation, colour intensity), and then reduce these to two components representing traits important in intra- and inter-sexual selection, respectively.

Effect sizes larger than $r = 0.30$ are rare in behavioural ecology, even for well-established relationships like those between sexually selected traits and reproductive success (Jennions et al. 2001; Møller and Jennions 2002). Several authors (e.g. Gontard-Danek and Møller 1999; Jennions et al. 2001) argue that low observed values are due to a high degree of noise and stochastic variation affecting biological relationships. For example, females may have strong mate preferences that might not be realized because preferred males are unavailable in a particular site or year, or because other females have already attached themselves to these males (Jennions et al. 2001). The extent to which noise contributes to diminishing an effect size estimate can be quantified experimentally (Gontard-Danek and Møller

1999), in the laboratory if possible, by exactly replicating the experiment with a different group of animals each time (see Kelly 2006a). If effect sizes of $r = 0.37 - 0.45$ are the best we can achieve for well-established relationships in intensely-studied organisms, like those measured here, it is not surprising we typically find small effect sizes in evolutionary ecology studies (Møller and Jennions 2002).

I conclude by suggesting that an examination of the effect sizes generated in this meta-analysis can provide an index that allows us to explore how well we know our study species, within the constraints imposed by unaccountable sources of variation.

Effect size by taxon

My results show that, in general, males with greater RHP own better territories. This effect was strongest (and significant) for insects, birds and amphibians but not so for fishes. The lack of a strong effect in fishes may stem from the fact that contests for territories are often settled based on residency. For example, Jones (1981) showed that male-male fights in *Pseudolabrus celidotus* wrasses are won by the resident male. Therefore, although female choice is based on territory quality, stochastic processes – random settlement – ultimately determine male reproductive success. Perhaps this is a general phenomenon among fishes, or at least among marine teleosts living on coral reefs (Nijman and Heuts 2000). Similarly, males with larger RHP accrued greater reproductive success overall but this effect was strongest (and significant) for insects, birds and amphibians.

Traits representing male dominance and resource quality

Among the studies I examined, body size was the most common trait studied by investigators as a predictor of male RHP, followed by signals (e.g. song repertoire size, tail length), weaponry, male age, body condition and ‘other’ (e.g. arrival date). That traits representing male RHP accounted for only 14% of the variation in resource-value and reproductive success, respectively, suggests that investigators may be misidentifying the relevant traits, or that factors other than phenotype, are important for controlling resources and accruing reproductive success. For example, arrival date may dictate male reproductive success. In birds, earlier-arriving individuals often acquire better territories and phenotypic traits, such as body size, need not be correlated with time of arrival (e.g. Hasselquist 1998).

All six types of RHP-traits showed a strong effect on a male’s ability to hold high-value resources with both older and better-conditioned males holding better resources. That males in better condition are able to hold a better resource is understandable given competition for territories is often

energetically demanding. The apparent success of older males is more difficult to explain; perhaps correlates of age, such as body size, are the actual causal factors responsible for the observed relationships (Brooks and Kemp 2001).

Males that accrue greater reproductive success tend to be in better condition or have greater signal value. Conversely, male age exhibited the weakest effect on reproductive success. This result was unexpected given that older animals in some taxa (e.g. mammals) tend to be larger and larger animals, which have greater RHP, are often found to have greater reproductive success (Andersson 1994). Contrary to this notion, however, is a growing body of empirical evidence showing that older animals may be less preferred by females (e.g. Hunt et al. 2004) and/or suffer in male-male competition (e.g. Forsyth and Montgomerie 1987), possibly due to reduced energy stores (e.g. Marden and Waage 1990).

For the subset of species discussed above, the observed intraspecific differences in effect size and sign among the three relationships could be real or they could reflect inaccurate identification of the relevant trait(s). Moreover, because many of the studies used in this meta-analysis relied on natural phenotypic variation and were correlative, several confounding factors were not controlled. For example, population demography (e.g. male density, Borgia 1980; McLain 1992; operational sex ratio, Blanckenhorn et al. 2003), individual state (e.g. energy levels, Marden and Waage 1990; Plaistow and Siva-Jothy 1996), local environmental conditions (e.g. temperature, Switzer 2002) and ecological factors (e.g. level of predation risk, Gwynne and O'Neill 1980) are all known to influence a male's tenure on a territory. The best way to combat problems associated with confounding factors and misidentification of important traits is to systematically manipulate different male traits and resource characters and then test which has the greatest effect on male reproductive success. Implementing this approach, however, is not always possible if working on a large animal or one that requires large territories. Perhaps, the best we can do is to quantify the relationship of interest in several populations throughout the breeding season to assess the generality of the relationship (Kelly 2006a).

Ultimately, investigators need to test all three relationships within the same species in order to appropriately determine the underlying mechanism responsible for a male's reproductive success. For example, that a male with apparently large RHP has high mating success does not necessarily mean that he controls more-valuable resources – females may prefer males with larger trait values independent of resource characteristics – nor does it mean that he will have greater reproductive success if females use the sperm of other males (Fig. 1) (Candolin 2003). Testing the strength of all three relationships, however, will compound the problems associated with testing a single relationship,

particularly because factors affecting male tenure vary spatiotemporally. To reduce error associated with differences in location and time of year, researchers should test the three relationships concurrently at the same site. In the seed bug *Neacoryphus bicrucis*, for example, the advantage of male body size in defending territories and acquiring mates decreases as population density increases from early- (mid-April) to mid-season (early May) (McLain 1992). At higher densities, (i.e. early May) the otherwise positive correlation between resource value and male body size (RHP) breaks down with males eventually abandoning resource-defence and entering into scramble competition. Therefore, if the three main relationships examined in the present meta-analysis were studied at different times of the year in *N. bicrucis* an inaccurate picture could emerge regarding the importance of male body size and resource value on male mating success. In the rare case that an investigator has tested all three relationships within a species, they have apparently recognized the potential confounds and examined all relationships concurrently at the same location (18/22 species, Table 4). Very few studies have experimentally tested the interrelationships of male RHP, resource-value and male mating or reproductive success in the laboratory or used partial correlations to statistically account for potentially confounding factors (Lindström 1992; Kelly 2006b).

In conclusion, (i) investigators must quantify within a species each of the three relationships addressed in this meta-analysis and test the alternative hypotheses outlined in Fig. 1 Scenario 1–3; (ii) studies require larger sample sizes ($N > 52$) to detect statistically significant relationships; (iii) once the putatively important trait(s) has been identified (by using a correlative approach and relying upon natural phenotypic variation), manipulative experiments with proper controls and reciprocal treatments (i.e. good male on poor resource and vice versa) should be employed, preferably in the laboratory in order to illuminate the independent effects of male phenotypic traits and resource characteristics on male reproductive success (at the very least we should statistically control for confounding variables (i.e. resource characteristics and male traits) by using analysis of covariance or partial correlations); (iv) investigators must control for spatiotemporal factors in field studies by testing each relationship at the same time and place; (v) investigators should quantify the degree to which biological noise contributes to relationships by conducting experiments (sensu Gontard-Danek and Møller 1999); (vi) we need to expand the list of taxa used to address the above hypotheses, in particular, we need more studies on fishes, reptiles, amphibians, crustaceans and mammals; and finally (vii) because we are ultimately interested in the benefits to male fitness of holding a particular resource or possessing particular traits, we need accurate measures of mating success.

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