

LOUISE M. ALISSA

Efeito da limitação de sítios reprodutivos sobre a intensidade da seleção sexual e a qualidade do cuidado paternal: uma meta-análise

Effect of reproductive site limitation on the intensity of sexual selection and the quality of paternal care: a meta-analysis



Fonte: Frank Leo (2015)

SÃO PAULO

2018

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selection and the quality of paternal care: a meta-analysis**

Dissertação apresentada ao Instituto de
Biotecnologia da Universidade de São Paulo como
parte dos requisitos para obtenção do título de
Mestre em Ciências, na área de Ecologia de
Ecossistemas Terrestres e Aquáticos.

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Resumo

ALISSA, L.M. **Efeito da limitação de sítios reprodutivos sobre a intensidade da seleção sexual e a qualidade do cuidado paternal: uma meta-análise.** 2018. Dissertação (Mestrado) – Instituto de Biociências, Universidade de São Paulo, SP.

A disponibilidade de sítios reprodutivos influencia tanto o comportamento de machos quanto de fêmeas em espécies cujo sistema de acasalamento depende da defesa de recursos. Usando uma abordagem meta-analítica, testamos cinco previsões direta ou indiretamente relacionadas à teoria de sistemas de acasalamento. Esperávamos que a limitação de sítios reprodutivos promoveria: (1) aumento na competição masculina pela posse de recursos; (2) aumento na variância do sucesso reprodutivo dos machos, gerando valores alto de oportunidade para a seleção sexual; (3) aumento da intensidade da seleção sobre características masculinas relacionadas à posse de recursos; (4) aumento no risco de competição espermática e (5) diminuição da qualidade do cuidado paternal. Compilamos informações de estudos observacionais e experimentais que compararam o comportamento reprodutivo de indivíduos da mesma espécie em situação de alta e baixa disponibilidade de sítios reprodutivos. Encontramos que, quando os sítios reprodutivos são escassos, há um ligeiro aumento na competição masculina, com maiores taxas de roubo de ninhos e interações agonísticas, e um ligeiro aumento no gradiente de seleção sobre características masculinas, com machos bem sucedidos tendendo a ser maiores do que machos mal sucedidos em monopolizar recursos. A disponibilidade de sítios reprodutivos não teve nenhum efeito consistente sobre a oportunidade para a seleção sexual e o risco de competição espermática. Entretanto, machos territoriais investiram mais em gônadas e perderam menos paternidade quando os sítios reprodutivos eram escassos. Não encontramos nenhum efeito da disponibilidade de sítios reprodutivos sobre a qualidade do cuidado paternal. Em conjunto, nossos resultados indicam que as previsões sobre como a disponibilidade de sítios reprodutivos influencia diversos aspectos de sistemas de acasalamento baseados na defesa de recursos têm fraco respaldo empírico. Tais previsões não consideram a plasticidade nas táticas de acasalamento de machos e fêmeas, tornando-as demasiadamente simplistas. Adicionalmente, desde a formulação original da teoria de sistemas de acasalamento, nossa compreensão sobre competição espermática aumentou. Sabemos atualmente que previsões acuradas sobre a intensidade e direção da seleção sexual devem levar em consideração processos pré- e pós-copulatórios. Finalmente, a interconexão entre seleção sexual e cuidado parental é complexa e a teoria original de sistemas de acasalamento não provê elementos suficientes para a construção de previsões claras e de amplo escopo taxonômico.

Palavras-chave: competição entre machos, competição espermática, defesa de recursos, limitação de recursos, paternidade, potencial ambiental para a poliginia, sistema de acasalamento, táticas alternativas de reprodução.

Abstract

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ALISSA, L.M. **Effect of reproductive site limitation on the intensity of sexual selection and the quality of paternal care: a meta-analysis.** 2018. Dissertação (Mestrado) – Instituto de Biociências, Universidade de São Paulo, SP.

The availability of reproductive sites is a major factor shaping the behavior of males and females in species with resource-based mating systems. Using a meta-analytic approach, we tested five predictions directly or indirectly derived from the mating system theory. We expected that reproductive site limitation would lead to: (1) intense male-male competition for resource possession; (2) high variance in male reproductive success, generating high values of opportunity for sexual selection; (3) high intensity of selection on male traits related to resource possession; (4) high sperm competition risk; and (5) low quality of paternal care. We compiled information from observational and experimental studies that compared the reproductive behavior of individuals of the same species under low and high reproductive site limitation. We found that, when reproductive sites are limited, there is a slight increase in male-male competition, with higher rates of nest takeover and agonistic interactions, and a slight increase in the selection gradient on male traits, with successful males tending to be larger than unsuccessful males. Reproductive site limitation has no consistent effect on the opportunity for sexual selection and on the sperm competition risk. However, territorial males invest more in gonads and lose less paternity when reproductive sites are limited. There is also no clear effect of reproductive site limitation on the quality of paternal care, but few studies have addressed this subject. Taken together, our findings indicate that predictions on how reproductive site limitation affects several aspects of resource-based mating systems have weak empirical support. These predictions do not consider the plasticity in the mating tactics of males and females, which make them too simplistic. Moreover, since the original proposition of the mating system theory, our understanding of sperm competition increased a lot. We now know that accurate predictions on the intensity and direction of sexual selection should take into account both pre- and post-copulatory processes. Finally, the interplay between sexual selection and parental care is complex, and the original framework of mating system theory does not provide sufficient elements to derive clear and taxonomically broad predictions.

Key-words: alternative reproductive tactics, environmental potential for polygyny, male-male competition, mating system, parental effort, paternity, resource defense, resource limitation, sperm competition.

77 **Effect of reproductive site limitation on the intensity of sexual**
78 **selection and the quality of paternal care: a meta-analysis***

79

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86	CONTENTS	
87	I. Introduction	05
88	II. Methods	15
89	1. Definitions	15
90	2. Literature search and inclusion criteria	15
91	3. Effect size calculation	17
92	4. Data coding and moderators	18
93	5. Statistical analyses	20
94	6. Heterogeneity and publication bias	21
95	III. Results	22
96	1. Prediction 1: Male-male competition	22
97	2. Prediction 2: Opportunity for sexual selection	24
98	3. Prediction 3: Selection on male trait	24
99	4. Prediction 4: Sperm competition risk	25
100	5. Prediction 5: Quality of paternal care	29
101	6. Publication bias	29
102	IV. Discussion	33
103	1. Male-male competition	33
104	2. Intensity of sexual selection	36
105	3. Selection under male trait	40
106	4. Sperm competition risk	43
107	5. Quality of paternal care	47
108	V. Conclusions	49
109	VI. Acknowledgements	51
110	VII. References	52
111	VIII. Supporting Information	65
112		

113 I. INTRODUCTION

114 In 2017, the seminal paper by Emlen & Oring (1977) entitled "Ecology, sexual selection and
115 evolution of mating systems" completed 30 years with more than 3700 citations in the *Web of*
116 *Science* and 5659 in *Google Scholar*, being the most cited article on sexual selection in both
117 databases (Figure 1). This paper was a groundbreaking contribution for several reasons. First, the
118 authors formalized the concept of mating system of a population, which "refers to the general
119 behavioral strategy employed in obtaining mates". According to the original definition, the
120 mating system encompasses "the number of mates acquired, the manner of mate acquisition,
121 the presence and characteristics of any pair bonds, and the patterns of parental care provided by
122 each sex". Second, the authors proposed a classification of the avian mating systems that was
123 based on the ecological and behavioral potential to monopolize mates, and on the ways through
124 which such monopolization takes place. This classification and the nomenclature proposed by
125 Emlen & Oring (1977) were embraced for researchers working with other animal groups
126 (including invertebrates) and are widely used until present days. Third, the authors linked the
127 degree of female monopolization to the intensity of sexual selection. According to them, "the
128 ability of a portion of the population to control the access of others to potential mates [...]
129 accounts for the differing intensities of sexual selection found in different species and,
130 frequently, between populations of the same species". Thus, the greater the potential for mate
131 monopolization, the higher should be the intra-population variation in mating success and,
132 consequently, the potential intensity of sexual selection. This has been perhaps the most
133 intensively explored aspect of the mating system theory.

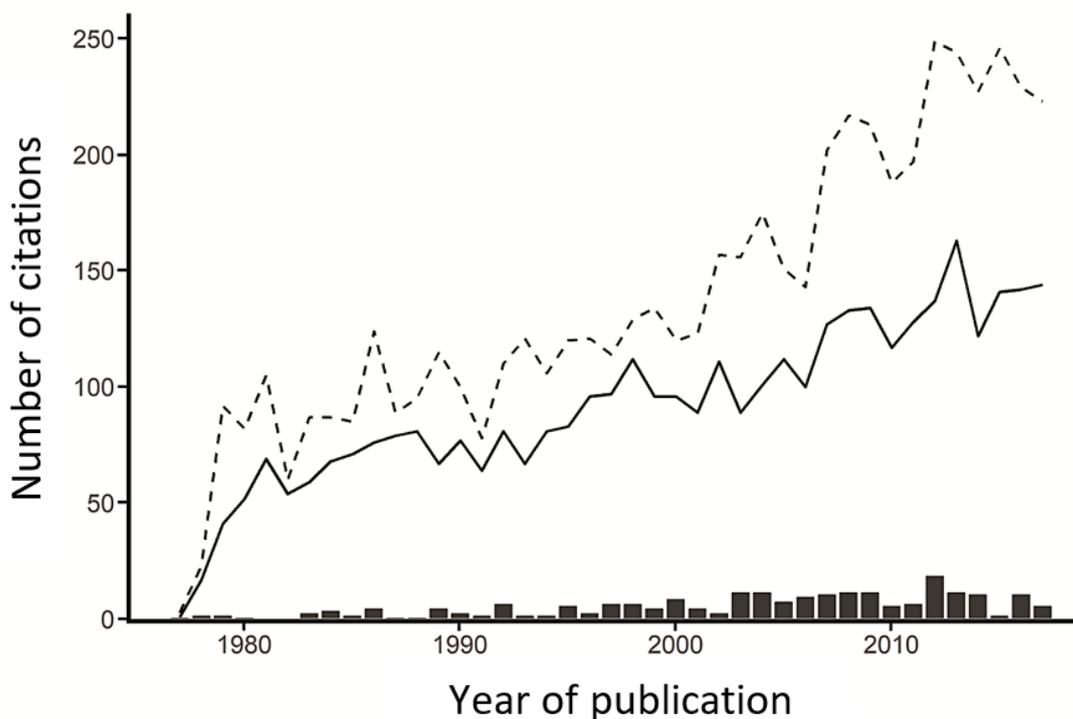
134 The general framework of the mating system theory can be summarized as follow (based
135 on Emlen & Oring, 1977; see also Davies, 1991 and Reynolds, 1996). Female reproductive success
136 in many species usually depends on food acquisition and access to suitable reproductive sites.
137 Thus, females tend to be spatially associated with places where critical resources (food and/or
138 reproductive sites) are more available or have higher quality. Male reproductive success, in turn,

139 usually depends on the encounter with potential mating partners. Thus, males tend to be
140 spatially associated with places where females are more abundant. If the critical resources
141 needed for females are spatially clumped and can be economically defended, some males may
142 monopolize these resources and have exclusive access to most of the females. Other ecological
143 factor that influences mate monopolization is the degree of synchrony in female sexual
144 receptivity. If all females in a population become sexually receptive at the same time, individual
145 males will have low chance of monopolizing multiple mates. However, with increasing
146 asynchrony in female sexual receptivity in a population, individual males will have higher chance
147 of monopolizing multiple mates. In conclusion, the spatial distribution of critical resources and
148 the temporal distribution of receptive females are the two most important determinants of the
149 *environmental potential for polygamy* (EPP), which refers to the ecological conditions that allow
150 some individuals to acquire multiple mates in a population.

151 According to the mating system theory, the EPP should determine the variation in the
152 number of mates per males and, ultimately, the type of mating system found in a population
153 (Emlen & Oring, 1977; Davies, 1991). One criticism about the concept of EPP relies on the fact
154 that, when critical resources are clumped, their monopolization by males can be either easier or
155 more difficult. Indeed, the EPP proved to be difficult to measure and, since the original
156 proposition of the concept, there was no attempt to identify universal parameters that determine
157 the EPP and make it comparable between different animal groups (Shuster, 2009; Kokko *et al.*,
158 2014). This may explain why the term EPP has been infrequently mentioned in the literature on
159 mating systems (Fig. 1). Nowadays, it seems clear that the EPP depends on species-specific
160 features that will determine the payoffs of male-male competitive interactions (Kokko *et al.*,
161 2014). Thus, empirical studies aiming to evaluate how the availability of critical resources
162 influences the intensity of sexual selection and the organization of mating systems are focused
163 on individual species and rarely address EPP. These empirical studies either compare
164 populations where resource availability shows natural variation or experimentally manipulate

165 resource availability under field or laboratory conditions (Table 1). In most cases, the critical
166 resources are reproductive sites used by females to lay eggs, and the study species comprise a
167 wide variety of animal groups, including arthropods, fish, amphibians, and birds (Table 1).
168 Following the classical theory, regardless of the group, reproductive site limitation should lead
169 to increased male-male competition and high intensity of sexual selection (Predictions 1 and 2,
170 respectively, in Table 2).

171



172

173 **Fig. 1.** Number of citations of the paper on mating systems by Emlen & Oring (1977) in two databases:
174 *Google Scholar* (dashed line) and *Web of Science* (solid line). In both databases the paper is the most cited
175 when we use "sexual selection" as the sole search term. The bars refer to the number of papers that
176 mention the term "environmental potential for polygyny" or "environmental potential for polygamy" in
177 their content (the result of this search is based only on the *Google Scholar* database).

178

179 Reproductive site limitation may also lead to three additional predictions that are not
180 directly based on the mating system theory. When reproductive sites are limited, and male-male
181 competition is intense, only large males or those bearing large armaments (e.g., horns, antlers,
182 forceps, or spines) should be able to monopolize the available reproductive sites and,
183 consequently, the access to receptive females (Prediction 3 in Table 2). This prediction is based
184 on the theory of animal contests and on the widespread pattern that larger males usually defeat
185 smaller males in intraspecific contests (examples in Clutton-Brock, 1982; Thornhill & Alcock,
186 1983; Andersson, 1994; Emlen, 2014). Small males, with no or poorly-developed armaments, are
187 usually unable to defend scarce reproductive sites, and should adopt reproductive tactics that
188 do not involve physical contests (Prediction 3 in Table 2). In fact, small males of many species
189 (both vertebrates and invertebrates) sneak copulations, act as satellites, or even mimic females
190 as a way to invade the few available reproductive sites defended by large males (examples in
191 Oliveira *et al.*, 2008). Thus, reproductive site limitation should increase the sperm competition
192 risk because the only chance of small males or large males without a territory to acquire
193 copulations is to invade the few available reproductive sites (Prediction 4 in Table 2). This
194 prediction is also based on the theory of alternative reproductive tactics and on growing
195 evidence that females of many species are highly polyandrous and accept copulations with other
196 males besides the territory owner (reviewed in Oliveira *et al.*, 2008; see also Taylor *et al.*, 2014).

197 In many species in which males defend reproductive sites, territorial defense is associated
198 with uniparental male care (Table 1). This is the case of several harvestman, fish, and frog species
199 (Lehtinen & Nussbaum, 2003; Ah-King *et al.*, 2005; Requena *et al.*, 2014). Among birds, in turn,
200 territorial males usually engage in biparental care, helping females to incubate eggs and feed the
201 nestlings (Table 1). As explained before, reproductive site limitation is expected to increase
202 sperm competition. This may happen either because of frequent territory invasions by small
203 males in fish or because of high rates of extra-pair copulations in birds (e.g., Cogliati *et al.*, 2014;
204 García-Navas *et al.*, 2014). Considering that sperm competition decreases paternity assurance,

205 reproductive site limitation should ultimately decrease the quality of paternal care because
206 males of many species are known to adjust their parental effort to the perceived paternity
207 (Sheldon, 2002; see also Griffin *et al.*, 2013). Moreover, when the competition for reproductive
208 sites is intense, territorial males should invest most of their time in territory defense to prevent
209 nest takeovers by rival males (e.g., Newton, 1994; Lindström, 2001). Thus, males are expected to
210 have higher energy expenditure in territory defense and lower foraging rate, which may decrease
211 the quality of parental care they provide, and ultimately decrease offspring survival (Prediction
212 5 in Table 2). These predictions on the quality of paternal care are not directly based on the
213 mating system theory, but they have already been explored in observational and experimental
214 studies on the consequences of reproductive site limitation in harvestmen, fish, and birds
215 (examples in Table 1).

216 After 30 years of empirical studies on mating systems with a wide variety of animal groups,
217 there is a surprisingly low number of articles that explicitly address how the availability of
218 reproductive sites influences male-male competition, the intensity of sexual selection, the sperm
219 competition risk, and the quality of paternal care (Table 1). Although scarce, these articles offer
220 the unique opportunity of testing key predictions directly or indirectly derived from the mating
221 system theory. This is the main goal of our study, in which we used a meta-analytic approach to
222 test the five predictions presented above and summarized in Table 2. Our dataset includes
223 species from several groups of invertebrates and vertebrates that occur in a great variety of
224 habitats worldwide (Table 1). To our knowledge, this is the first quantitative review focusing on
225 the effect of reproductive site limitation on the organization of mating systems. The findings
226 reported here are a formal test of the generality of the patterns predicted by the theory and
227 enhance our understanding of how reproductive site limitation may affect several aspects of
228 resource-based mating systems.

229 **Table 1.** List of species included both in the qualitative synthesis and in the quantitative analyses, with information on the type of reproductive site, type of mating
 230 system, and type of parental care. We also provide information on the type of resource limitation (*number* of sites, *spatial distribution* of sites, or *quality* of sites),
 231 the methodological approach (Obs. = observational or Exp. = experimental; Lab. = laboratory or Field conditions), and the habitat and country where the studies
 232 were conducted. The references marked with an asterisk were not included in the quantitative analyses (see reasons for exclusion in Table S2 on online Appendix
 233 1).

234

Taxon	Reproductive site	Mating system#	Parental care	Resource limitation	Methodological approach	Habitat, Country	References
Arthropoda							
<i>Homarus gammarus</i> (Decapoda)	Natural cavities in rocks	Polygamy	Maternal	Number	Exp. (Lab.)	Oceanic coast, UK	Debuse <i>et al.</i> , 2003
<i>Neacoryphus bicrucis</i> (Hemiptera)	Host plants	Polygamy	No care	Quality	Obs. (Field)	Grassland, USA	McLain, 1992*
<i>Scatophaga stercoraria</i> (Diptera)	Dung pats	Polygamy	No care	Number	Exp. (Field)	Pastures, USA	Borgia, 1980, 1982
<i>Magnispina neptunus</i> (Opiliones)	Natural cavities in roadside banks	Polygamy	Maternal	Number	Exp. (Lab.)	Rain forest, Brazil	Werneck, 2011
<i>Serracutisoma proximum</i> (Opiliones)	Host plants at river margins	Polygamy	Maternal	Number	Exp. (Field)	Rain forest, Brazil	Muniz & Machado, 2015
<i>Hemideina crassidens</i> (Orthoptera)	Natural cavities in fallen logs	Polygamy	Maternal	Quality	Exp. (Field)	Rain forest, New Zealand	Kelly, 2007

235

Taxon	Reproductive site	Mating system#	Parental care	Resource limitation	Methodological approach	Habitat, Country	References
Actinopterygii							
<i>Archocentrus nigrofasciatus</i> (Perciformes)	Natural cavities in rocks	Monogamy	Biparental	Number	Exp. (Field + Lab.)	Freshwater, Nicaragua	Gumm & Itzkowitz, 2007; Cleveland-Roberts & Itzkowitz, 2009*; Lehtonen & Lindstrom, 2008
<i>Cichlasoma panamense</i> (Perciformes)	Natural cavities in stream banks	Monogamy	Biparental	Number	Obs. (Field)	Freshwater, Panama	Townshend & Wootton, 1985
<i>Cottus bairdi</i> (Scorpaeniformes)	Natural cavities in rocks and logs	Polygamy	Paternal	Quality	Exp. (Field)	Freshwater, USA	Downhower & Brown, 1980
<i>Cottus cognatus</i> (Scorpaeniformes)	Natural cavities under rocks	Polygamy	Paternal	Number	Obs. (Field)	Freshwater, Canada	Mousseau & Collins, 1987
<i>Cottus pollux</i> (Scorpaeniformes)	Natural cavities in rocks	Polygamy	Paternal	Number	Exp. (Lab.) + Obs. (Field)	Freshwater, Japan	Natsumeda <i>et al.</i> , 2012; Natsumeda, 2013
<i>Gobiusculus flavescens</i> (Perciformes)	Natural cavities in rocks and mussel shells	Polygamy	Paternal	Number	Exp. (Lab.)	Oceanic coast, Sweden	Mück <i>et al.</i> , 2013; Wacker & Amundsen, 2014
<i>Lamprologus callipterus</i> (Perciformes)	Snail shells	Polygamy	Maternal	Quality	Exp. (Lab.) + Obs. (Field)	Freshwater, Zambia and Zaire	Maan & Taborsky, 2008*; Sato, 1994*
<i>Padogobius martensi</i> (Perciformes)	Natural cavities under rocks	Polygamy	Paternal	Number	Obs. (Field)	Freshwater, Italy	Lugli <i>et al.</i> , 1992
<i>Parablennius sanguinolentus</i> (Perciformes)	Natural cavities in rocks	Polygamy	Paternal	Quality	Obs. (Field)	Oceanic coast, Azores	Oliveira <i>et al.</i> , 2000

Taxon	Reproductive site	Mating system#	Parental Care	Resource limitation	Methodological approach	Habitat, Country	References
<i>Pimephales promelas</i> (Cypriniformes)	Aquatic plants	Polygamy	Paternal	Number	Obs. (Field)	Freshwater, USA	Bessert <i>et al.</i> , 2007
<i>Pomatoschistus microps</i> (Perciformes)	Mussel shells	Polygamy	Paternal	Number	Exp. (Lab.)	Oceanic coast, Sweden	Borg <i>et al.</i> , 2002 Forsgren <i>et al.</i> , 1996; Lindström & Seppa, 1996*;
<i>Pomatoschistus minutus</i> (Perciformes)	Shells and natural cavities in rocks	Polygamy	Paternal	Number, Distribution	Exp. (Field + Lab.) + Obs. (Field)	Oceanic coast, Finland and Sweden	Jones <i>et al.</i> , 2001a,b; Lindström 2001; Lehtonen & Lindström, 2004; Singer <i>et al.</i> , 2006; Klug <i>et al.</i> , 2010a
<i>Porichthys notatus</i> (Batrachoidiformes)	Natural cavities under rocks	Polygamy	Paternal	Number	Exp. + Obs. (Field)	Intertidal zone, EUA and Canada	DeMartini, 1988; Cogliati <i>et al.</i> , 2014
<i>Rhodeus amarus</i> (Cypriniformes)	Mussel shells	Polygamy	No care	Number	Exp. (Lab.)	Freshwater, Czech Republic and Poland	Przybylski <i>et al.</i> , 2007; Reichard <i>et al.</i> , 2008, 2009; Konečná <i>et al.</i> , 2010
<i>Rhodeus ocellatus</i> (Cypriniformes)	Gills of living mussels	Polygamy	No care	Number	Exp. (Lab.)	Freshwater, China	Casalini <i>et al.</i> , 2010
<i>Rhodeus sericeus</i> (Cypriniformes)	Gills of living mussels	Polygamy	No care	Number	Exp. (Lab.)	Freshwater, UK	Mills & Reynolds, 2003
<i>Salaria pavo</i> (Perciformes)	Natural cavities in rocks	Polygamy	Paternal	Number, Distribution	Exp. (Lab.) + Obs. (Field)	Freshwater, Portugal	Almada <i>et al.</i> , 1994*; Saraiva <i>et al.</i> , 2009, 2012

242 **Table 1.** Continued.

243

Taxon	Reproductive site	Mating system#	Parental Care	Resource limitation	Methodological approach	Habitat, Country	References
<i>Tautoga onitis</i> (Labridae)	Natural cavities in rocks	Polygamy	No care	Number	Exp. (Lab.)	Oceanic coast, USA	Olla <i>et al.</i> , 1981*
<i>Tridentiger brevispinis</i> (Perciformes)	Natural cavities under rocks	Polygamy	Paternal	Number	Exp. (Field)	Freshwater, Japan	Takahashi, 2008
Amphibia							
<i>Dendrobates pumilio</i> (Anura)	Phytotelmata and pudles	Polygamy	Maternal	Number	Obs. (field)	Rain forest, Costa Rica	Pröhl, 2002
Aves							
<i>Calonectris diomedea</i> (Procellariiformes)	Natural cavities in rocks	Monogamy	Biparental	Number	Obs. (field)	Coastal plain, Azores	Bried <i>et al.</i> , 2010*
<i>Cyanistes caeruleus</i> (Passeriformes)	Natural cavities in tree trunks	Polygamy, monogamy	Biparental	Number	Exp. (field)	Deciduous forest, Austria and France	Jacot <i>et al.</i> , 2009; Charmantier & Perret, 2004; Garcia-Navas <i>et al.</i> , 2014
<i>Sialia mexicana</i> (Passeriformes)	Natural cavities in tree trunks	Monogamy	Biparental	Number	Exp. + Obs. (field)	Boreal forest, USA	Duckworth, 2006
<i>Sialia sialis</i> (Passeriformes)	Natural cavities in tree trunks	Monogamy	Biparental	Number	Exp. (field)	Grassland, USA	Gowaty & Bridges 1991; Stewart <i>et al.</i> , 2010
<i>Tachycineta bicolor</i> (Passeriformes)	Natural cavities in tree trunks	Monogamy	Biparental	Number	Exp. (field)	Deciduous forest, Canada	Conrad <i>et al.</i> , 2001

244 # We used the term "polygamy" instead of polygyny because in all species included in the table both males and females are know to mate multiple times.

245 **Table 2.** Predictions directly or indirectly derived from the mating system theory and that were tested in
246 this study using a meta-analytic approach.
247

Prediction 1: Male-male competition

Prediction: the higher the limitation of reproductive sites, the more pronounced should be male-male competition for the possession of these sites.

Expected results for response variables: in places where reproductive site limitation is high, we expect higher values of: (a) frequency of agonistic interactions between males for territory (i.e., reproductive site) possession, (b) proportion of time that territorial males invest in repelling rival males, (c) mean duration of agonistic interactions between males, (d) frequency of territory takeovers, and (e) rate of territory occupancy by males.

Prediction 2: Opportunity for sexual selection

Prediction: the higher the limitation of reproductive sites, the higher the variation in the reproductive success of males in a population and, consequently, the more intense should be the sexual selection.

Expected results for response variables: metrics of opportunity for sexual selection (such as I_s and I_{mates}) should have higher values in places where reproductive site limitation is high.

Prediction 3: Selection on male traits

Prediction: the higher the limitation of reproductive sites, the more intense should be the selection on traits that allow males to monopolize these sites and have exclusive access to receptive females.

Expected results for response variables: in places where reproductive site limitation is high, we expect that: (a) the selection gradient on male body and armament size should be steeper, and (b) the mean values of body and armament size of successful males should be higher.

Prediction 4: Sperm competition risk

Prediction: the higher the limitation of reproductive sites, the higher the sperm competition risk because the only chance of small males or large males without a territory to acquire mates is to invade the few available sites and copulate with females that have already copulated with the territory owner.

Expected results for response variables: in places where reproductive site limitation is high, we expect higher values of: (a) gonadal investment or ejaculate rate of territory males, (b) frequency of sneaking attempts and territory invasions, and (c) occurrence of extra-par copulations. Consequently, (d) the average paternity loss should be higher in places where reproductive sites limitation is high.

Prediction 5: Quality of paternal care

Prediction: the higher the limitation of reproductive sites, the most time and energy males should invest in territory defense, which may decrease both the quality of paternal care and offspring survival.

Expected results for response variables: in places where reproductive site limitation is high, we expect that estimates of offspring survival and male offspring attendance and should be lower.

248

249 II. METHODS

250 1. Definitions

251 In the literature on mating system, the term "reproductive site" includes a great variety of places,
252 such as nests actively built by parental individuals, natural cavities in rocks, corals, tree trunks,
253 and fallen logs, phytotelmata, dung pats, mussel shells, host plants, and subaquatic vegetation
254 (Table 1). In the present study, we formally defined reproductive site as a discrete patch of
255 habitat that can be defended by a male and that is important for female reproduction, more
256 specifically for oviposition. Moreover, we considered three situations in which reproductive sites
257 can be limited, and thus may affect the degree of female monopolization by males: (1) when
258 there is low number of reproductive sites with similar quality; (2) when the spatial distribution
259 of reproductive sites with similar quality is clumped; and (3) when there is low number of high-
260 quality reproductive sites (Table 1). Although most of the empirical studies we found in the
261 literature focuses on the first situation, there are some studies that experimentally manipulated
262 the spatial distribution or the quality of the reproductive sites available to the males (Table 1).

263

264 2. Literature search and inclusion criteria

265 We conducted a literature search for relevant studies based on the PRISMA protocol (Preferred
266 Reporting Items for Systematic Reviews and Meta-Analyses, see [http://www.prisma-
267 statement.org/](http://www.prisma-statement.org/)). We searched the literature in *Web of Science* and *Google Scholar*, considering
268 all articles published between 1977 and March 2018. The combination of keywords used for each
269 search are specified in Table S1 (online Appendix 1). We also searched for all articles that cited
270 Emlen & Oring (1977) in *Google Scholar*. From the resultant list of articles, we read their titles
271 and abstracts searching for information on natural and/or experimental differences in the
272 number, spatial distribution, and quality of reproductive sites (Fig. S1 in online Appendix 1).
273 Moreover, the articles should mention some measure of male-male competition (Prediction 1),

274 opportunity for sexual selection (Prediction 2), selection gradient on male traits (Prediction 3),
275 sperm competition risk (Prediction 4), and/or quality of paternal care (Prediction 5). When the
276 necessary information was found, or at least there was an indication that the data provided in
277 the study could be useful, we considered the article as "potential" and proceeded to full reading.
278 In these cases, we also searched the list of references (backward search) and citation records
279 (forward search) of the selected articles in an attempt to obtain additional studies. All articles
280 considered as "potential", regardless of they were used or not in the quantitative synthesis, were
281 included in the qualitative review presented in Table 1 (see also Fig. S1 in online Appendix 1).

282 To include an article in the quantitative analyses, it should attend the following criteria:
283 (i) males of the study species should compete for the access of a reproductive site, charactering
284 a resource-based mating system; (ii) the methodological approach could be observational or
285 experimental, conducted either under field or laboratory conditions, but there should be
286 variation in the number, spatial distribution, and/or quality of reproductive sites between
287 populations, sites, or experimental groups; (iii) the results should provide information on how
288 reproductive site limitation affects male-male competition, the opportunity for sexual selection,
289 the selection gradient on male traits, the sperm competition risk, and/or the quality of paternal
290 care; (iv) the reported data should provide sufficient information to calculate effect sizes. The
291 reasons for exclusion of some articles that attended the inclusion criteria are listed in online
292 Appendix 1 (see section "VIII. Supporting Information").

293

294 3. Effect size calculation

295 Excepting for Prediction 2 (see below), the direction and magnitude of the effect of reproductive
296 site limitation (predictor variable) on the response variables (listed in Table 2) were quantified
297 with the Z_r effect size, which is a Fisher's transformation of the correlation coefficient r
298 (Nakagawa & Cuthill, 2007; Harisson, 2011). We opted for the Z_r , instead of more usual effect
299 sizes based on standardized mean differences (e.g., Hedges' g), because this measure is less
300 affected by extreme differences between situations of low and high reproductive site limitation,
301 and also because it satisfied many assumptions of our meta-analytical models (Koricheva *et al.*,
302 2013; Santos *et al.*, 2017).

303 To calculate effect sizes, we gave preference to use contingency tables, frequencies, means,
304 measures of data dispersion (standard error, standard deviation, or variance), and sample sizes.
305 In some cases, we needed to extract data from figures, usually box-plots, using the software
306 *ImageJ* (<https://imagej.nih.gov/ij/>). We also contacted several authors requesting data or
307 additional information not presented in their articles. If descriptive statistics were lacking, we
308 calculated effect sizes from inferential statistics, using t -values and F -values associated with
309 degrees of freedom or sample sizes (following Lipsey & Wilson, 2001 and Nakagawa & Cuthill,
310 2007). This last method was particularly important to calculate effect sizes based on measures
311 of selection gradients on male traits (Prediction 3) because many studies reported differences
312 between slopes using only inferential statistics. We used well-established formulas in the
313 literature to convert the data extracted from the studies to r (Lipsey & Wilson, 2001; Nakagawa
314 & Cuthill, 2007; Koricheva *et al.*, 2013).

315 To generate each r value, we compared the values of the response variable under *low* (or
316 *no*) reproductive site limitation (either site, population, or experimental group) with the values
317 of the response variable under *high* reproductive site limitation. After that, we used the function
318 `escalc()` from the package *metafor* (Viechtbauer, 2010) to transform r values in Z_r and its 95%

319 confidence interval (95% CI). Thus, *positive values* of effect sizes indicate that a response variable
320 has higher values *when reproductive site limitation is high*. In turn, *negative values* of effect sizes
321 indicate that a response variable has higher values *when reproductive site limitation is low*. Zero
322 indicates that reproductive site limitation has no detectable effect on the response variable (see
323 the expected results for each prediction in Table 2).

324 As mentioned before, to test Prediction 2, we did not use Z_r as the effect size measure. In
325 this case, the information collected in the primary studies was the opportunity for sexual
326 selection (I), a standard measure of variance in mating (I_{mates}) or reproductive success (I_s) that
327 has no dimension and is rarely accompanied by dispersion measures (Jones, 2009). Because it is
328 difficult to convert I values in conventional effect sizes, we used the natural logarithm of the
329 coefficient of variation ratio (lnCVR) as the measure of effect size (following Nakagawa *et al.*,
330 2015 and Janicke *et al.*, 2016). By calculating the ln of the ratio between the I value in the situation
331 of *high* reproductive site limitation and the I value in the situation of *low* reproductive site
332 limitation, we obtained positive and negative values. Positive values indicate that the
333 opportunity for sexual selection is higher when reproductive site limitation is high, whereas
334 negative values indicate that the opportunity for sexual selection is lower when reproductive site
335 limitation is high. We estimated variance (V) as $V = 1/N-3$, where N is the total number of males
336 used to calculate I (following Kraaijeveld *et al.*, 2011 and Moura & Peixoto, 2013).

337

338 **4. Data coding and moderators**

339 For each article included in the meta-analyses we coded the following information: (a) type of
340 mating system exhibited by the study species, including social/sequential monogamy and
341 polygamy, which includes all cases of resource defense polygyny in which both males and
342 females are promiscuous; (b) type of parental care, including maternal, paternal, biparental, and
343 no care; and (c) methodological approach, which could be observational and/or experimental,

344 conducted under field and/or laboratory conditions (Table 1). These variables were used as
345 moderators in the meta-analyses of all predictions because, in theory, they could influence the
346 intensity of male-male competition, the opportunity for sexual selection, the slope of selection
347 gradients on male traits, the sperm competition risk, and the quality of paternal care (Clutton-
348 Brock, 1982, 1999; Andersson, 1994; Simmons, 2001; Shuster & Wade, 2003).

349 We also used specific variables as moderators for each prediction. For Prediction 1, we
350 used the type of male-male competition, which we classified as: (a) direct, including measures
351 of agonistic behaviors, such as frequency or rate of fights, nest takeovers, and attacks to
352 intruders; and (b) indirect, including measures of competition for reproductive sites, such as
353 occupation rate and proportion of new nests occupied. For Prediction 2, we used *I* values based
354 on paternity analyses (i.e., number of legitimate offspring) or observational data (i.e., number of
355 mates or total number of eggs inside the nests). For Prediction 3, we used the type of male trait,
356 which we classified into two groups: (a) body size, including body mass, total body length,
357 carapace length, etc.; and (b) armament size, including claw volume, maxilar width, etc. For
358 Prediction 4, we used the type of proxy of sperm competition risk measured in the articles, which
359 we classified into three groups: (a) frequency of alternative reproductive tactics (ARTs) or extra-
360 pair copulations (EPCs), including variables related to the number of attempts of territory
361 invasion by sneaker males, presence of sneaker males inside the territory, relative frequency of
362 males exhibiting ARTs in the population, number of EPCs, etc.; (b) gonadal investment,
363 including measures of territorial male investment in gonadal mass, ejaculation rate, and sperm
364 release; and (c) paternity loss, including the proportion or frequency of illegitimate offspring
365 based on paternity analyses. Finally, for Prediction 5, we identified if the decrease of paternal
366 care quality was related to: (a) costs paid by the parental males, including reductions in life span
367 and foraging frequency, and increases in non-parental activities, such as nest defense; or (b)
368 costs paid by the offspring, including increases in mortality or feeding rate.

369

370 5. Statistical analyses

371 In Table 2, we present the predictions we tested and describe the most common response
372 variables used in the articles. During effect size calculations, we gathered information related to
373 each prediction in the articles included in our analyses. For each prediction, we conducted an
374 individual meta-analysis including all individual effect sizes to calculate an overall effect size.
375 We expected positive values of mean effect size for Predictions 1 to 4, and negative values of
376 mean effect size for Prediction 5.

377 Because the same species and the same article could provide more than one effect size to
378 each analysis, and because data from multiple species are statistically dependent due to shared
379 evolutionary history, we performed multi-level (mixed model) meta-analyses, including the
380 phylogeny of the species (see Fig. S2 in online Appendix 1), the identity of the species, and the
381 identity of the articles as random variables. The identity of effect sizes was also included as a
382 random variable to calculate the residual heterogeneity (as proposed by Nakagawa & Santos,
383 2012). As an alternative approach, we performed a model selection of the four random variables.
384 The results of the meta-analyses using this alternative approach were qualitatively the same as
385 those obtained using all random variables, and differences in the estimates and their respective
386 95% CI using the two approaches were in the decimals (online Appendix 2, see section "VIII.
387 Supporting Information"). Thus, we present only the results obtained with the models
388 containing all random variables, so that we could be explicit about the proportion of variance
389 explained by each of them.

390 As fixed factors, we used several moderators to account for important biological or
391 methodological factors that could influence the magnitude and perhaps the direction of the
392 effect sizes (see section "4. Data coding and moderators"). In Table 3, we report the results of
393 models that include moderators, together with the p-values of a *Q-test* (Q_m), which is a variance
394 alike statistical test. It is important to highlight that we tested the moderators one at a time and

395 that we did not include any kind of interaction between them due to the low number of effect
396 sizes in some predictions. In the results reported below, mean meta-analytic effects (Zr) close to
397 0.10 were considered small, values close to 0.3 were considered medium, and values higher than
398 0.5 were considered large (following Cohen, 1988). All analyses were performed using the
399 package *metafor* (Viechtbauer, 2010) and the software R version 3.4.1 (R Development Core
400 Team, 2016).

401

402 **6. Heterogeneity and publication bias**

403 We used an extended version of I^2 index to quantify the heterogeneity in the data attributed to
404 sampling error ($I^2 = 0\%$ means that all variation in the data is associated with sampling error; I^2
405 $= 100\%$ means that there is no variation associated with sampling error). Using this index, we
406 partitioned the total heterogeneity in the data amongst different sources: variation explained by
407 the phylogeny, species identity, article identity, and residual variation, i.e., the variation between
408 effect sizes that remains to be explained by the predictor variables (Nakagawa & Santos, 2012).
409 To estimate the phylogenetic signal in the effect size estimative, we calculated the phylogenetic
410 heritability index, H^2 , which is similar to Pagel's λ (Pagel, 1999; Nakagawa & Santos, 2012).

411 Finally, to check publication bias in our dataset, we first visually inspected the funnel plots,
412 which plot the effect sizes against their respective standard error. A symmetric distribution of
413 points in the funnel plots indicates no publication bias (Egger *et al.*, 1997, Stern & Egger, 2001).
414 We also formally tested the existence of publication bias with the Egger's regression method.
415 According to this method, an intercept that does not differ from zero suggests lack of publication
416 bias (Stern & Egger, 2005; Koricheva *et al.*, 2013).

417

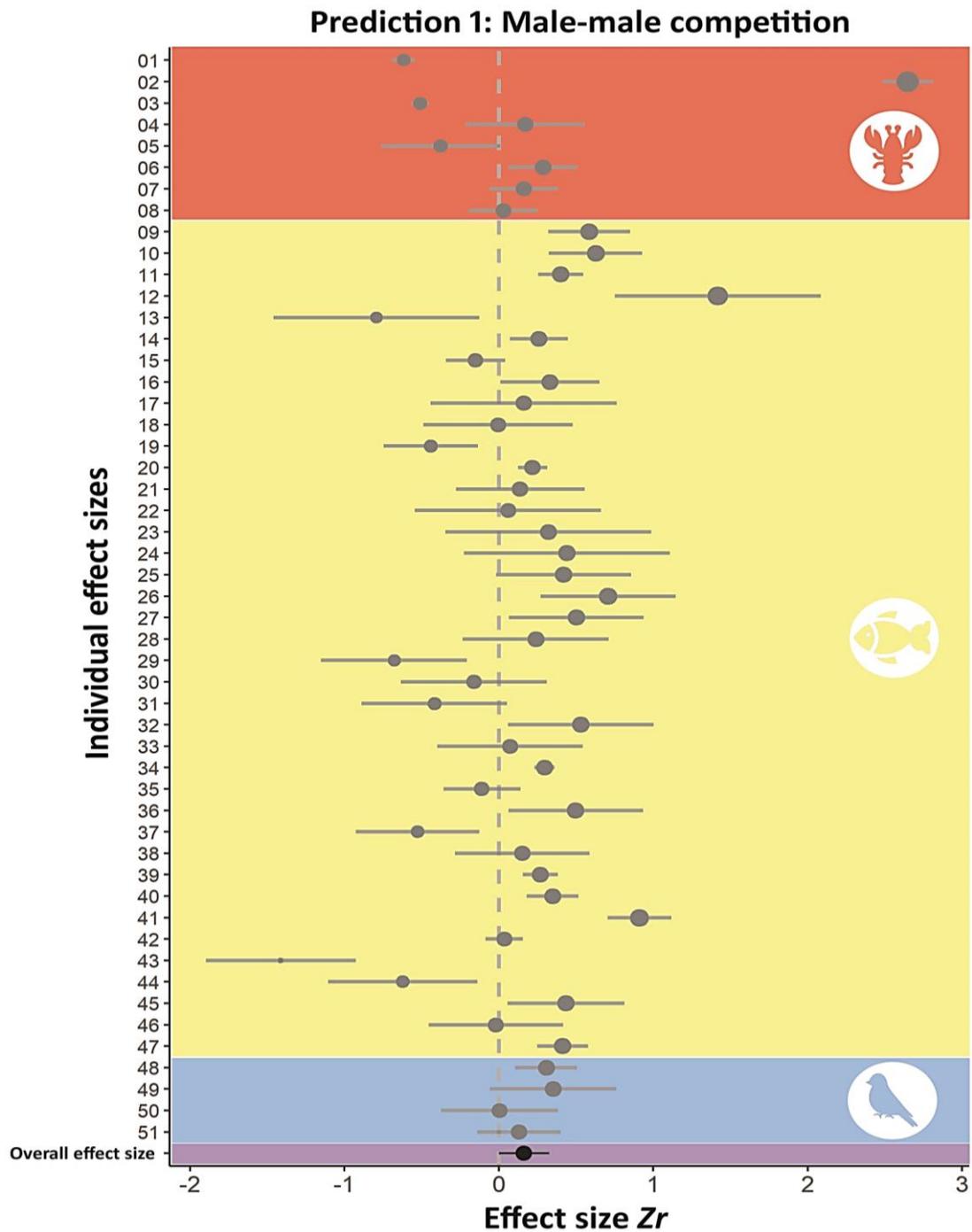
418 III. RESULTS

419 The dataset used in the quantitative analyses includes 35 articles derived from our search in the
420 *Web of Science* and *Google Scholar* and 9 articles derived from the backward and forward
421 searches. The dataset also includes information from one unpublished thesis of our research
422 group. Thus, we compiled a total of 45 studies (Fig. S1 in online Appendix 1) from which we
423 calculated 226 effect sizes. The selected studies refer to 28 species belonging to 13 orders,
424 including both invertebrates and vertebrates (Table 1).

425

426 1. Prediction 1: Male-male competition

427 This analysis included 20 species (arthropods = 3, fish = 14, birds = 3) studied in 25 articles, from
428 which we extracted 51 effect sizes. The overall meta-analytic effect Z_r was positive, but the
429 magnitude of this value was small ($Z_r = 0.1633$, 95% CI = -0.0002 to 0.3268). This result indicates
430 that, in situations of high reproductive site limitation, there is a slight increase in male-male
431 competition (Fig. 2). Total heterogeneity of effect sizes was high, and almost all of this was
432 residual variance to be explored by the moderators ($I^2_{\text{total}} = 97.21\%$, $I^2_{\text{phylogeny}} < 0.001\%$; $I^2_{\text{study}} <$
433 0.001% ; $I^2_{\text{species}} < 0.001\%$; $I^2_{\text{between effect sizes, residuals}} = 97.21\%$). The phylogenetic signal was
434 insignificant ($H^2 < 0.001\%$), and none of the moderators we used explained a significant part of
435 the variation in the data (Table 3). However, studies performed under field conditions (Fig. 7A)
436 and with species exhibiting paternal care (Fig. 7B) seem to generate slightly larger effect sizes
437 (Table 3). The specific moderator related to the type of male-male competition was non-
438 significant (Table 3).



439

440 **Fig. 2.** Forest plot for Prediction 1: effect of reproductive site limitation on male-male competition. Grey
 441 points and lines represent values of individual effect sizes and their 95% confidence intervals, respectively.
 442 The black point and line represent the value of the overall meta-analytic effect and its 95% confidence
 443 interval, respectively. The vertical dashed line indicates effect size = 0. Different background colors
 444 indicate effect sizes from three animal groups: arthropods (red), fish (yellow), and birds (blue).

445

446 2. Prediction 2: Opportunity for sexual selection

447 This analysis included 17 species (arthropods = 4, fish = 11, frogs = 1, birds = 1) studied in 22
448 articles, from which we extracted 48 effect sizes. The overall meta-analytic effect was positive
449 ($\ln\text{CVR} = 0.324$), but the confidence interval of this estimate crossed zero (95% CI = -0.121 to
450 0.771). This result indicates that there was no clear effect of reproductive site limitation on the
451 values of opportunity for sexual selection (Fig. 3). Total heterogeneity of effect sizes was high
452 ($I^2_{\text{total}} = 99.16\%$; $I^2_{\text{phylogeny}} = 4.33\%$; $I^2_{\text{study}} < 0.001\%$; $I^2_{\text{species}} < 0.001\%$; $I^2_{\text{between effect sizes, residuals}} = 94.83\%$),
453 and the phylogenetic signal was weak ($H^2 = 4.33\%$). None of the moderators explained a
454 significant part of the variation in the data (Table 3). However, we have an indication that effect
455 sizes calculated with data from species with maternal care are, consistently, positive (Fig. 7C).
456 Finally, mean effect sizes based on data with or without paternity information were not different
457 in magnitude or direction. It is important to note, though, that we have an underrepresentation
458 of studies that calculate I using paternity information, which comprise, approximately, 10 % of
459 all effect sizes (Table 3).

460

461 3. Prediction 3: Selection on male traits

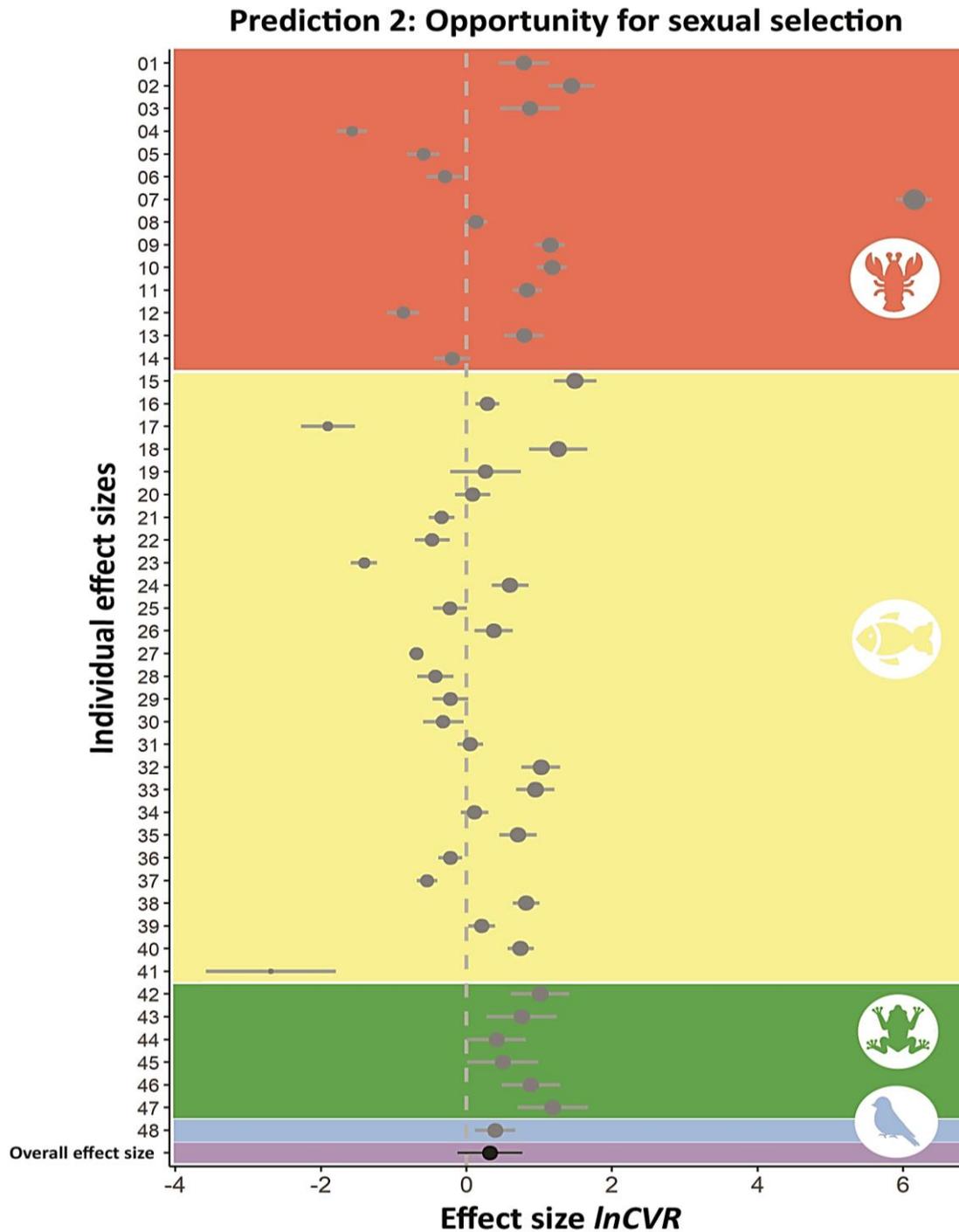
462 This analysis included 15 species (arthropods = 4, fish = 9, birds = 2) studied in 20 articles, from
463 which we extracted 69 effect sizes. The overall meta-analytic effect Zr was positive, but the
464 magnitude of this value was small ($Zr = 0.133$, 95% CI = 0.028 to 0.237). This result indicates that,
465 in situations of high reproductive site limitation, successful males have traits related to resource
466 monopolization slightly larger than unsuccessful males (Fig. 4). Total heterogeneity of effect
467 sizes was high ($I^2_{\text{total}} = 93.06\%$; $I^2_{\text{phylogeny}} < 0.001\%$; $I^2_{\text{study}} < 0.001\%$; $I^2_{\text{species}} < 0.7\%$; $I^2_{\text{within effect size, residuals}} = 92.03\%$), and the phylogenetic signal was insignificant ($H^2 < 0.001\%$). The moderator
469 methodological approach was significant, indicating that observational studies provided larger
470 values of effect size when compared with experimental studies (Fig. 7D). We also have an

471 indication that effect sizes calculated with data from polygamous species are consistently
472 positive (Fig. 7E). Regarding the specific moderator, the mean effect based on measures of body
473 size was one order of magnitude larger than the mean effect based on measures of armament
474 size (Fig. 7F). It is important to note, though, that we have an underrepresentation of studies
475 that estimate selection gradient on armaments, which comprise only 13% of all effect sizes (Table
476 3).

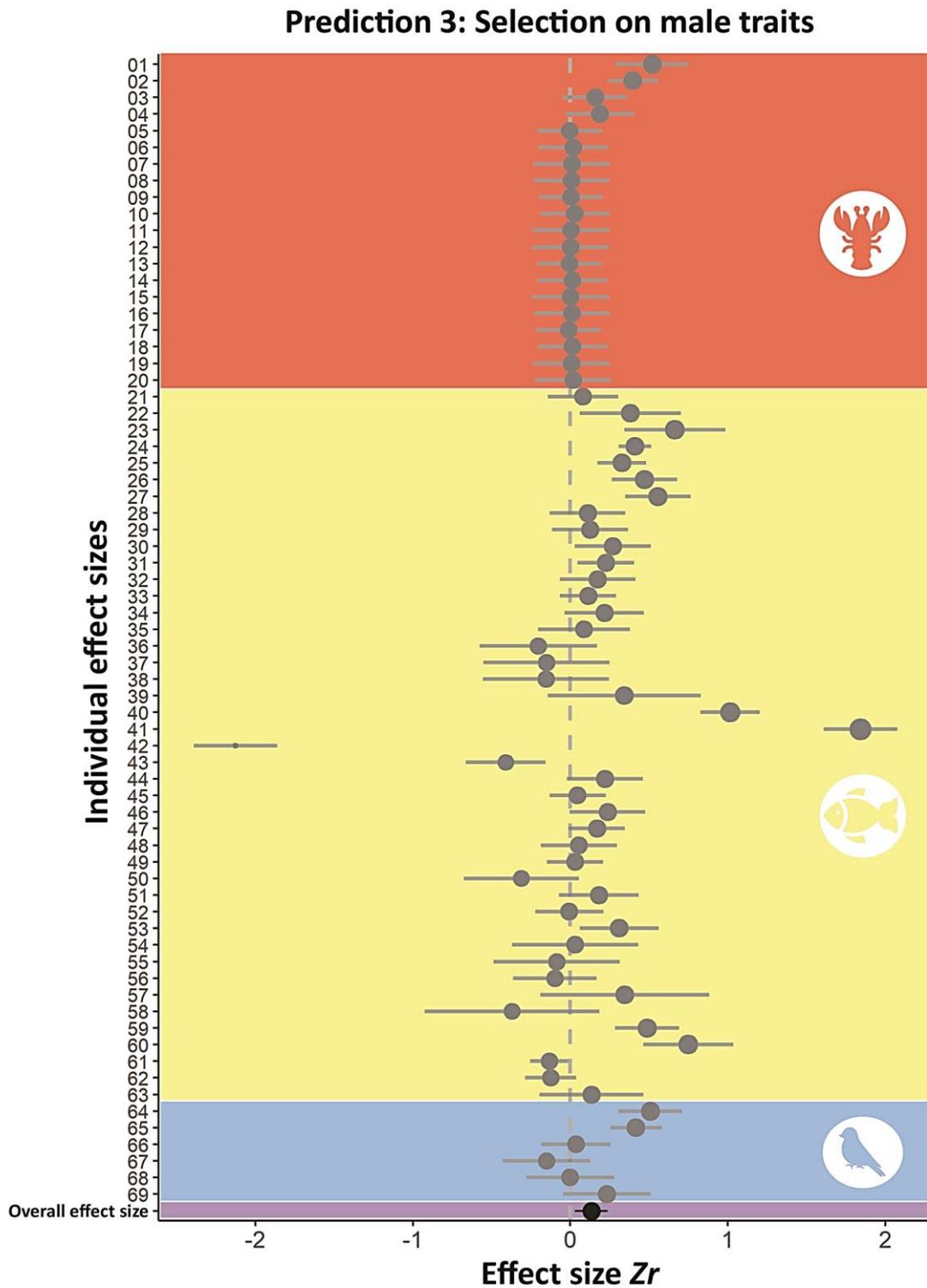
477

478 **4. Prediction 4: Sperm competition risk**

479 This analysis included 13 species (arthropod = 1, fish = 9, birds = 3) studied in 19 articles, from
480 which we extracted 39 effect sizes. The overall meta-analytic effect was negative, but close to
481 zero ($Zr = -0.039$), and the confidence interval crossed zero (95% CI = -0.197 to 0.119). This result
482 indicates that there is no clear tendency of increased sperm competition risk in situations of
483 high reproductive site limitation (Fig. 5). Total heterogeneity of effect sizes was high ($I^2_{\text{total}} =$
484 79.68%) and, contrary to the results obtained in the previous predictions, a more balanced part
485 of the heterogeneity in the data was explained by the random variables ($I^2_{\text{phylogeny}} = 16.34\%$; I^2_{study}
486 $< 0.001\%$; $I^2_{\text{species}} = 31.64\%$; $I^2_{\text{within effect size, residuals}} = 31.69\%$). Moreover, the phylogenetic signal was
487 moderated when compared with the other predictions ($H^2 = 19.59\%$). The moderators related to
488 the type of mating system, type of parental care, and methodological approach were non-
489 significant (Table 3). However, the specific moderator related to the type of proxy used to
490 measure sperm competition risk accounted for part of the heterogeneity in the data (Table 3).
491 Effect sizes calculated based on frequencies of ARTs or EPCs were small, whereas effect sizes
492 calculated based on measures of gonadal investment were moderate (both with positive values).
493 In turn, effect sizes calculated based on paternity loss had moderately negative values (Fig. 7G).



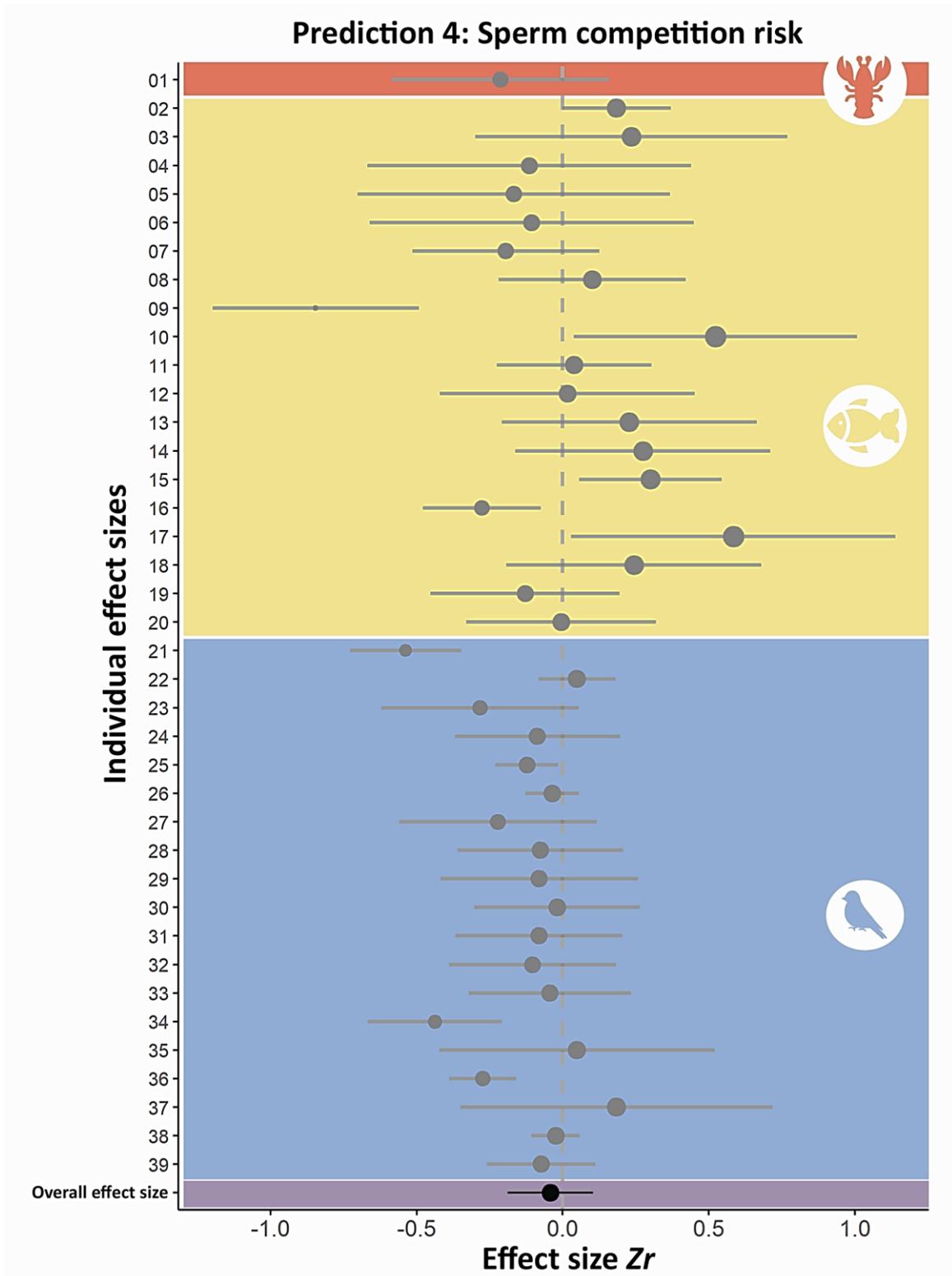
494
 495 **Fig. 3.** Forest plot for Prediction 2: effect of reproductive site limitation on the opportunity for sexual
 496 selection. Grey points and lines represent values of individual effect sizes and their 95% confidence
 497 intervals, respectively. The black point and line represent the value of the overall meta-analytic effect and
 498 its 95% confidence interval, respectively. The vertical dashed line indicates effect size = 0. Different
 499 background colors indicate effect sizes from four animal groups: arthropods (red), fish (yellow), frogs
 500 (green), and birds (blue).
 501



502

503 **Fig. 4.** Forest plot for Prediction 3: effect of reproductive site limitation on the selection on male traits.
 504 Grey points and lines represent the values of individual effect sizes and their 95% confidence intervals,
 505 respectively. The black point and line represent the value of the overall meta-analytic effect and its 95%
 506 confidence interval, respectively. The vertical dashed line indicates effect size = 0. Different background
 507 colors indicate effect sizes from three animal groups: arthropods (red), fish (yellow), and birds (blue).

508



509

510 **Fig. 5.** Forest plot for Prediction 4: effect of reproductive site limitation on sperm competition. Grey points
 511 and lines represent the values of individual effect sizes and their 95% confidence intervals, respectively.
 512 The black point and line represent the value of the overall meta-analytic effect and its 95% confidence
 513 interval, respectively. The vertical dashed line indicates effect size = 0. Different background colors
 514 indicate effect sizes from three animal groups: arthropods (red), fish (yellow), and birds (blue).

515

516 **5. Prediction 5: Quality of paternal care**

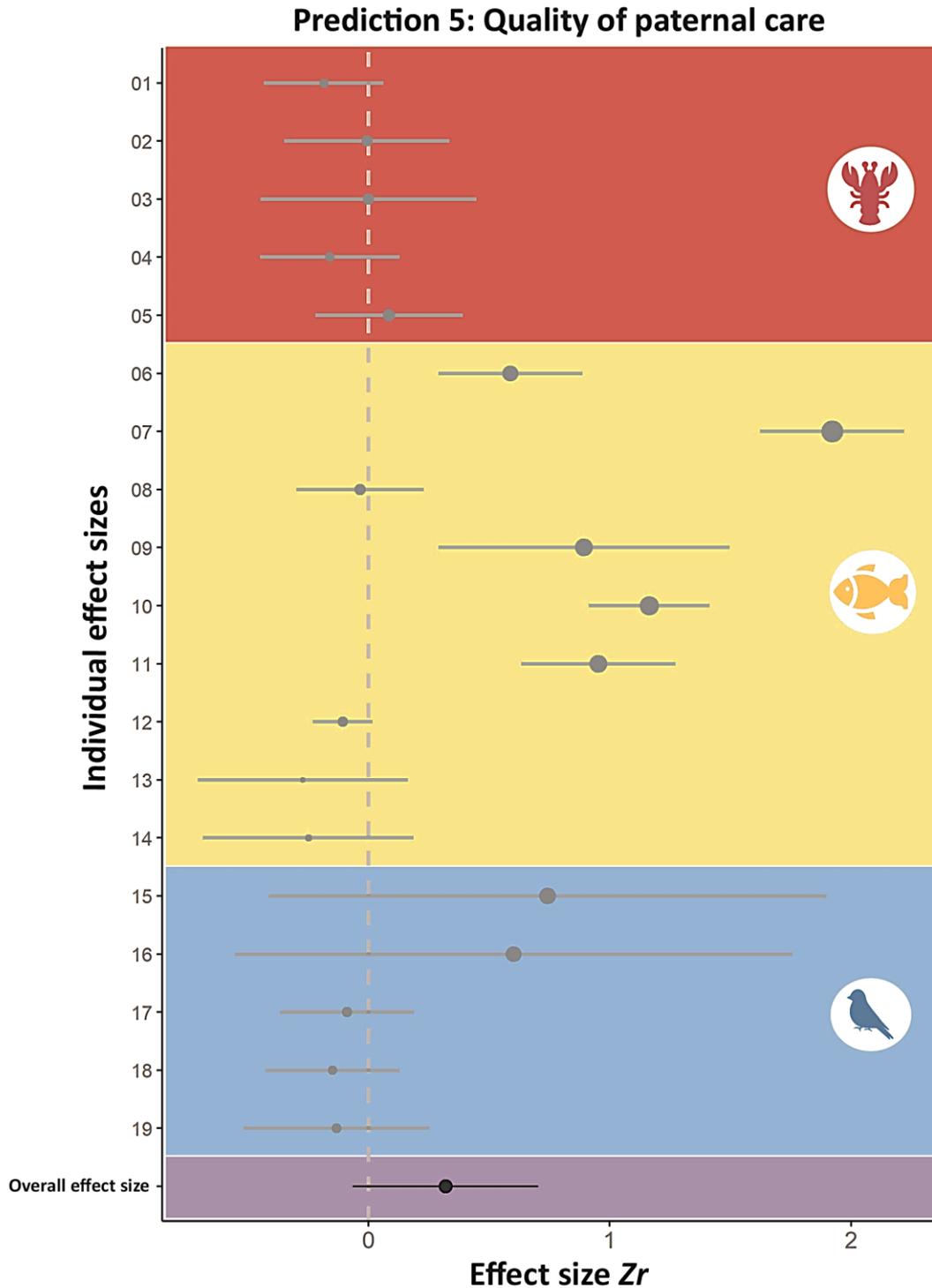
517 This analysis included 9 species (arthropod = 1, fish = 7, birds = 1) studied in 11 articles, from
518 which we extracted 19 effect sizes. The overall effect of reproductive site limitation on the quality
519 of paternal care was positive and moderate ($Zr = 0.319$, 95% CI = -0.064 to 0.704), but the
520 confidence interval crossed zero (Fig. 6). The total heterogeneity of effect sizes was high ($I^2_{\text{total}} =$
521 94.48%), but the random variables explained part of this variance ($I^2_{\text{phylogeny}} < 0.001\%$; $I^2_{\text{study}} =$
522 20.15%; $I^2_{\text{species}} = 47.75\%$; $I^2_{\text{within effect size, residuals}} = 26.57\%$). Moreover, the phylogenetic signal was
523 insignificant ($H^2 < 0.001\%$). None of the moderators explained a significant part of the variation
524 in the data (Table 3). In particular, effect sizes based on costs paid by parental males were not
525 different in magnitude or direction than the effect sizes based on costs paid by offspring (Table
526 3).

527

528 **6. Publication bias**

529 Based on a visual inspection of the funnel plots, the only meta-analysis that suggested
530 publication bias was that for Prediction 5 (Fig. S3 in online Appendix 1), which is the prediction
531 with the smallest number of articles and species included. However, the Egger's test does not
532 indicate publication bias for Prediction 5, but indicates publication bias for Prediction 3 ($p <$
533 0.05; Table S3 in online Appendix 1).

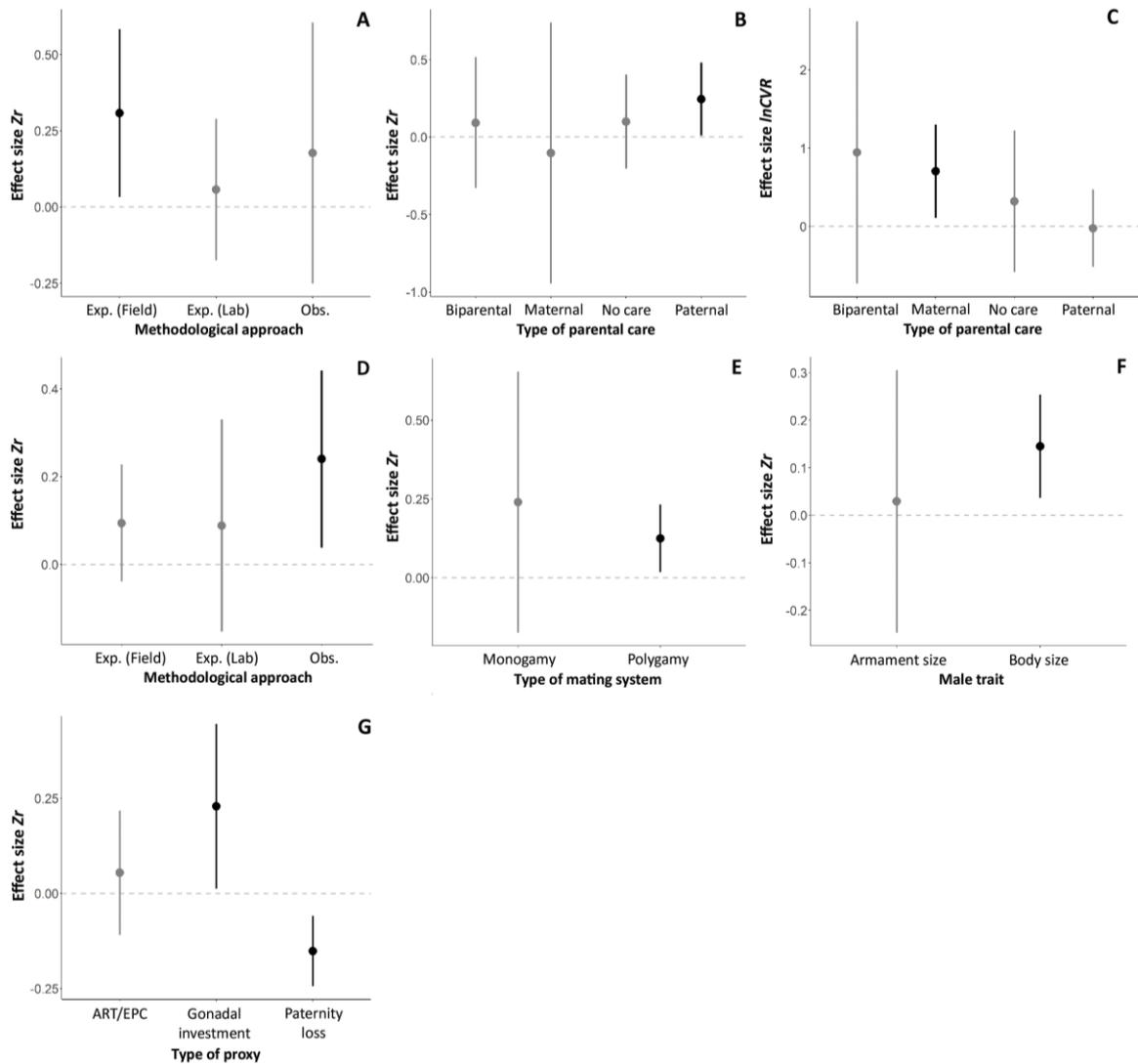
534



535

536 **Fig. 6.** Forest plot for Prediction 5: effect of reproductive site limitation on the quality of paternal care.
 537 Grey points and lines represent the values of individual effect sizes and their 95% confidence intervals,
 538 respectively. The black point and line represent the value of the overall meta-analytic effect and its 95%
 539 confidence interval, respectively. The vertical dashed line indicates effect size = 0. Different background
 540 colors indicate effect sizes from three animal groups: arthropods (red), fish (yellow), and birds (blue).

541



542
543 **Fig. 7.** Mean effect sizes and their 95% confidence intervals (95% CI) for moderators that explained part
544 of the variance in the data. Mean effect sizes in which the 95% CI does not cross zero are highlighted in
545 black. Positive values indicate that the variables are higher in situations of high reproductive site
546 limitation than in low reproductive site limitation. Negative values indicate that the variables are lower in
547 situations of high of reproductive site limitation than in low reproductive sites limitation. (A) Effect of
548 methodological approach in Prediction 1: field experiments generate higher effect sizes of male-male
549 competition. (B) Effect of the type of parental care in Prediction 1: species with paternal care generate a
550 higher effect sizes of male-male competition. (C) Effect of the type of parental care in Prediction 2: species
551 with maternal care generate positive values of effect size. (D) Effect of methodological approach in
552 Prediction 3: observational studies generate higher values of effect size related to the gradient selection
553 on male traits. (E) Effect of mating system in Prediction 3: polygamous species generate positive values of
554 effect sizes. (F) Effect of the type of male trait in Prediction 3: effect sizes based on measures of body size
555 are higher than the ones based on measures of armament size. (G) Effect of type of proxy in Prediction 4:
556 effect sizes based on measures of gonadal investment are positive, whereas effect sizes based on paternity
557 loss are negative.

558 **Table 3.** Summary of meta-analytic models that included moderators. For the five predictions, we tested the effect of the methodological approach, type of mating
559 system, and type of parental care on the direction and magnitude of effect sizes. The specific moderators for each prediction are detailed in the footnote. For each
560 level of each moderator we report the mean effect size (MES), standard error (s.e.), p-value, and sample size (N). *Q_m* refers to the p-value for the *Q*-test for the
561 moderator. We emphasize in bold p-values < 0.05.
562

Moderators	Levels	Prediction 1				Prediction 2				Prediction 3				Prediction 4				Prediction 5			
		MES	s.e.	p	N	MES	s.e.	p	N												
Methodological approach	Exp. (field)	0.308	0.140	0.028	17	1.656	1.233	0.179	18	0.094	0.068	0.166	40	-0.097	0.118	0.414	25	0.002	0.338	0.993	8
	Exp. (lab)	0.057	0.118	0.629	27	0.699	0.496	0.158	12	0.088	0.123	0.472	12	0.255	0.183	0.162	6	0.443	0.307	0.149	7
	Obs.	0.177	0.218	0.417	7	0.213	0.27	0.428	18	0.240	0.102	0.019	17	-0.153	0.135	0.256	8	0.555	0.354	0.116	4
<i>Q_m</i>		—	—	—0.127		—	—	0.283		—	—	0.048		—	—	0.119		—	—	—0.261	
Mating system	Monogamy	0.085	0.227	0.705	7	1.656	1.229	0.177	1	0.239	0.211	0.256	4	-0.096	0.084	0.254	16	0.660	0.352	0.060	5
	Polygamy	0.176	0.090	0.052	44	0.3	0.248	0.226	47	0.125	0.054	0.022	65	0.002	0.065	0.986	23	0.192	0.229	0.401	14
<i>Q_m</i>		—	—	0.142		—	—	0.224		—	—	0.391		—	—	0.493		—	—	0.1615	
Parental care	Biparental	0.092	0.214	0.667	8	0.943	0.855	0.270	2	0.151	0.187	0.419	7	-0.122	0.259	0.637	19	0.297	0.359	0.408	8
	Maternal	-0.102	0.430	0.811	2	0.703	0.303	0.020	16	0.013	0.144	0.927	18	-0.213	0.353	0.546	1	—	—	—	
	No care	0.099	0.155	0.520	16	0.319	0.459	0.486	7	0.266	0.256	0.299	3	0.309	0.261	0.237	6	—	—	—	
	Paternal	0.244	0.12	0.042	24	-0.025	0.252	0.920	23	0.195	0.111	0.079	41	-0.102	0.218	0.639	13	0.329	0.258	0.201	11
<i>Q_m</i>		—	—	0.308		—	—	0.139		—	—	0.385		—	—	0.370		—	—	0.314	
Specific moderator*	A	0.111	0.107	0.299	32	-0.1627	0.623	0.794	4	0.029	0.141	0.835	9	0.054	0.083	0.5112	8	0.164	0.283	0.561	6
	B	0.244	0.134	0.067	19	0.359	0.209	0.086	44	0.142	0.055	0.008	60	0.228	0.110	0.038	6	0.380	0.204	0.062	13
	C	—	—	—		—	—	—		—	—	—		-0.151	0.047	0.001	25	—	—	—	
<i>Q_m</i>		—	—	0.11		—	—	0.211		—	—	0.031		—	—	0.018		—	—	0.175	

563 * Prediction 1: direct (A) or indirect (B) male-male competition for reproductive sites. Prediction 2: measures of opportunity for sexual selection based on paternity
564 analyses (A) or observational data (B). Prediction 3: selection gradient on body size (A) or armament size (B). Prediction 4: sperm competition risk estimated as
565 the frequency of alternative reproductive tactics or extra-pair copulations (A), gonadal investment (B), or paternity loss (C). Prediction 5: costs paid by the parental
566 males (A) or by the offspring (B).

567 IV. DISCUSSION

568 In this study, we used a meta-analytic approach to test five predictions on how reproductive site
569 limitation may influence the male-male competition, the intensity of sexual selection, the sperm
570 competition risk, and the quality of paternal care in several animal groups with resource-based
571 mating systems. Despite the great number of studies published on mating systems (Fig. 1) and
572 the widespread assumption that resource limitation affects mate monopolization, we found a
573 surprisingly small number of studies that could be used in our meta-analyses. The pool of studies
574 that met our selection criteria has a bias for vertebrates, especially fish (Figs. 2-3), but for some
575 predictions birds and/or arthropods are also well-represented (Figs. 4-5). The final dataset
576 includes populations from different kinds of habitats, ranging from oceanic coast to freshwater
577 and from temperate grasslands to tropical rain forests. Nonetheless, although a great portion of
578 the animal diversity is found in the tropics, the database has an over-representation of studies
579 conducted in temperate zones (Table 1). In what follows, we discuss the results of each
580 prediction, comparing the observed patterns with what would be expected by the mating system
581 theory (Table 2). We also highlight how to improve our predictive power in future studies on
582 the effects of reproductive site limitation, indicating aspects that deserve more investigation or
583 a different theoretical approach.

584

585 1. Male-male competition

586 We focused our search on species with resource-based mating systems, for which reproductive
587 site limitation should be critical to mate monopolization, and thus for male reproductive
588 success. We expected a moderate or even strong effect of reproductive site limitation on male-
589 male competition because the mating system theory proposes that agonistic interactions
590 between males for access to reproductive sites should be intensified when these sites are scarce
591 (e.g., Emlen & Oring, 1977; Davies, 1991; Arnold & Duvall, 1994; Ruzzante *et al.*, 1996; Shuster &
592 Wade, 2003). However, the overall effect size that we found indicates only a slight increase in

593 male-male competition when reproductive sites are somehow limited (Fig. 2). Moreover, the
594 overall effect size shows little overlap with zero, suggesting that the reproductive site limitation
595 may have no effect on the intensity of male-male competition. Finally, the effect size of many
596 studies was negative, indicating that male-male competition decreased when reproductive site
597 limitation increased (Fig. 2). This finding indicates that the overall intensity of male-male
598 competition may depend on other factors that are not included in the original formulation of
599 the mating system theory. Some of these factors, such as male dominance hierarchy and
600 behavioral plasticity of both males and females, are explicitly mentioned in some articles
601 included in Table 1 and they will be briefly discussed below.

602 In resource-based mating systems, male-male competition is highly dependent on the
603 economical defensibility of resources. As reproductive sites become costly to obtain and
604 maintain due to increased male-male competition, males can change their behavior as a way to
605 attenuate the risk of injuries during territorial fights. In the yellow dung fly *Scatophaga*
606 *stercoraria*, for instance, males behave less aggressively with each other when dung pats (i.e.,
607 reproductive sites) are less abundant. A possible reason for this pattern is the establishment of
608 dominance hierarchies in the dung pats, so that when reproductive sites are scarce, smaller
609 males bypass the territories of larger males avoiding injuries related to frequent fights for dung
610 monopolization (Borgia, 1982). However, when reproductive sites are abundant, males are well-
611 distributed between dung pats, and even subdominant and small males can establish territories,
612 being aggressive against invaders (Borgia, 1982). Thus, the establishment of male dominance
613 hierarchy may attenuate the costs related to injuries during territorial fights and explain why
614 male-male competition is less intense in places where reproductive sites are scarce.

615 Studies conducted with two fish species belonging to the genus *Rhodeus* provide insights
616 on how behavioral plasticity of male reproductive tactics can also attenuate male-male
617 competition in places where reproductive sites are somehow limited. Females of both *Rhodeus*
618 species use living mussels as oviposition site, and both the availability and the spatial

619 distribution of these mussels were experimentally manipulated in the laboratory. In *R. sericeus*,
620 the resource-based mating system break down when just a few mussels are available for many
621 males. In this situation, all males start mating opportunistically, with as much as 20 males
622 sneaking a single spawning female (Mills & Reynolds, 2003). In *R. amarus*, males show great
623 behavioral flexibility when resources are clustered. Territorial males start investing more in
624 ejaculate than sneaker males, and behave aggressively only when female density close to their
625 nest sites is high (Konečná *et al.*, 2010). Plasticity in male behavior enables each individual to
626 change the allocation of energy and time between pre- and post-copulatory components in
627 response to specific environmental conditions. More specifically, when reproductive sites are
628 scarce, males may decrease investment in direct male-male competition for access to females
629 and increase investment in traits that enhance fertilization chances via sperm competition (see
630 topic "4. Sperm competition risk" below).

631 Female plasticity in the use of reproductive sites can also attenuate male-male
632 competition. If females face severe limitation of high-quality reproductive sites, one option is to
633 use sub-optimal reproductive sites. In the Azorean rock-pool blenny *Parablennius*
634 *sanguinolentus*, for example, females are plastic in their response to limitation of high-quality
635 nests, i.e., big rock crevices with small entrance. Whereas some females increase the courtship
636 rate of males holding high-quality nests, other females accept low-quality nests, but are choosier
637 about male body size, preferring larger males (Oliveira *et al.*, 2000). Thus, males that do not
638 engage in intense competition for the high-quality nests still have chance of obtaining mates. In
639 a similar way, a field experiment conducted with the harvestman *Serracutisoma proximum*
640 showed that females in plots where the host plants regularly used as oviposition sites were
641 removed start using new plant species that had never been recorded before. Males defending
642 territories on plants not regularly used achieve copulations, and thus male-male competition for
643 the preferred plants is attenuated (Muniz & Machado, 2015). It seems, therefore, that female

644 preference for reproductive sites can respond to the availability of these sites, which may affect
645 the intensity of male-male competition.

646 As a final remark, it is important to stress the putative influence of the operational sex
647 ratio (OSR) on the results reported here. Since the original paper by Emlen & Oring (1977), the
648 OSR is predicted to have a key role in modulating the intensity of male-male competition and
649 ultimately the opportunity for sexual selection (see also Kvarnemo & Ahnesjö, 1996; Moura &
650 Peixoto, 2013; Janicke & Morrow, 2018). More specifically, the intensity of male-male competition
651 should peak at intermediate values of OSR (reviewed in Weir *et al.*, 2001). In most studies
652 conducted under field conditions the authors quantified the availability of reproductive sites,
653 but they did not provide data on the OSR of the natural populations, which hampers solid
654 conclusions on the intensity of competition really faced by the males. Although we did not detect
655 any significant effect of the methodological approach (observational vs. experimental) in the
656 magnitude of the effect sizes (Table 3), we suggest that future observational studies should take
657 into account not only the natural availability of reproductive sites, but also the OSR of the
658 populations.

659

660 **2. Intensity of sexual selection**

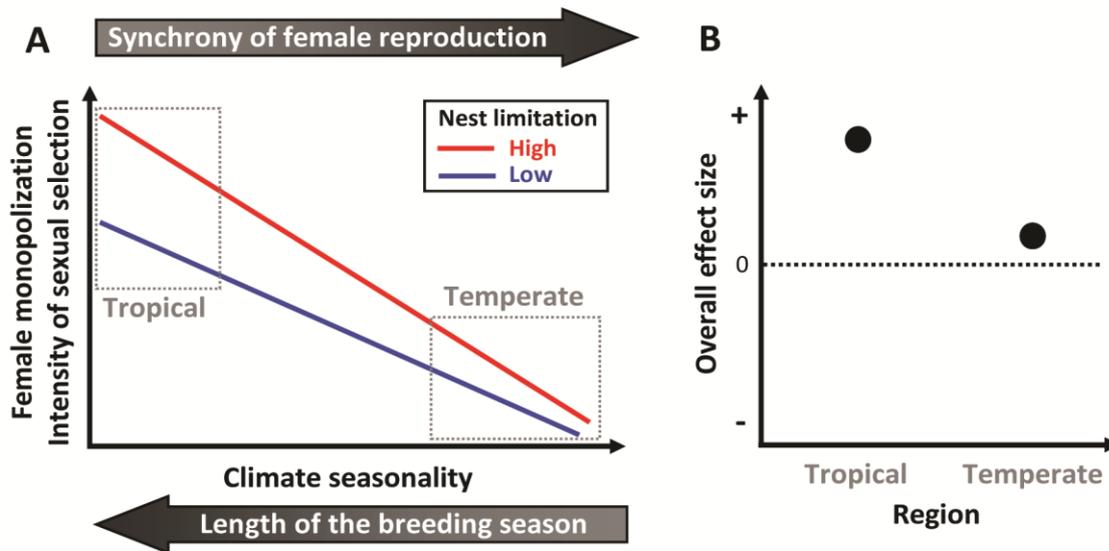
661 The use of the opportunity for sexual selection (I) as a metric of intensity of sexual selection has
662 been intensively debated in the last decade (e.g., Jones, 2009; Klug *et al.*, 2010b; Krakauer *et al.*,
663 2011; Jennions *et al.*, 2012). Although this debate is not the focus of our study, we stress that I is
664 expected to be informative about the intensity of sexual selection when mate monopolization is
665 strong (Klug *et al.*, 2010b), which is the case of species with resource-based mating systems
666 (Emlen & Oring, 1977; Wade, 1995; Ruzzante *et al.*, 1996, Shuster *et al.*, 2013). In fact, several
667 articles on the effects of reproductive site limitation use I as a measure of intensity of sexual
668 selection, and we took advantage of this information to compare sites with high and low
669 availability of reproductive sites. We expected to find higher variance in male mating and

670 reproductive success in sites where reproductive sites were limited, when compared with sites
671 where reproductive sites were not limited. However, we found great heterogeneity between
672 individual effect sizes, and an overall effect size with confidence interval that greatly overlaps
673 zero (Fig. 3). This finding indicates that there is no clear pattern of increased intensity of sexual
674 selection when reproductive sites are somehow limited.

675 In socially monogamous animals, such as most bird species, EPCs usually increase the
676 variance in male reproductive success, thus increasing the opportunity for sexual selection (e.g.,
677 Gibbs *et al.* 1990; Kempenaers *et al.*, 1992; Yezerinac *et al.*, 1995; Sheldon & Ellegren, 1999; but
678 see Webster *et al.*, 1995). However, among non-monogamous animals in which some males
679 exhibit ARTs, sneak copulations may decrease the opportunity for sexual selection. In fact,
680 empirical data coupled with a simple mathematical model showed that sneak copulations in the
681 polygamous sand goby *Pomatoschistus minutus* decrease the opportunity for sexual selection
682 (Jones *et al.*, 2001a). The dataset we used to test the prediction on the intensity of sexual selection
683 is almost entirely composed of polygamous arthropod, fish, and frog species (Fig. 3), most of
684 them exhibiting ARTs. If the same pattern described for the sand goby also occurs for some of
685 the polygamous species included in our dataset, the effect of reproductive site limitation on the
686 intensity of sexual selection would be the opposite than our original prediction (see Table 1). In
687 fact, the individual effect sizes calculated for several arthropod and fish species were negative,
688 indicating that the opportunity for sexual selection was lower when reproductive site limitation
689 was higher (Fig. 3). This finding suggests that the total variance in male reproductive success is
690 more influenced by the variance in post-mating success (i.e., egg fertilization) than by the
691 variance in pre-mating success (i.e., access to reproductive sites and females). The relationship
692 between pre- and post-mating selection has been rarely addressed in the literature (reviewed in
693 Shuster *et al.*, 2013), and we argue that an interesting question to be answered in future studies
694 is how each of these two episodes of sexual selection respond to reproductive site limitation in
695 polygamous species with resource-based mating systems.

696 An additional, non-mutually exclusive explanation for the lack of a clear pattern in the
697 overall effect size of opportunity for sexual selection is related to a geographic bias in the
698 occurrence of species in our dataset, which are mostly concentrated in temperate regions (Table
699 1). In general, populations or species living in temperate regions have a shorter breeding season
700 when compared to populations or species living in tropical regions (e.g., arthropods: Machado
701 *et al.*, 2016; frogs: Morrison & Hero, 2003; birds: Stutchbury & Morton, 1995). A short breeding
702 season leads to a more synchronous arrival of receptive females in the mating pool. When
703 females breed synchronously, their monopolization by males is expected to be more difficult
704 (e.g., Emlen & Oring, 1977; Ims, 1988; Grant, 1993), especially if the reproductive sites are scarce
705 or spatially clumped (Fig. 8A). In fact, there is comparative evidence for birds that EPCs are more
706 frequent in species in which females breed synchronously (Stutchbury & Morton, 1995). Thus,
707 even if reproductive sites are scarce or clumped, males may have lower potential for female
708 monopolization in species from temperate regions when compared to species from tropical
709 regions (Fig. 8A). Assuming that the maximum potential for female monopolization in our
710 dataset is constrained by female synchrony, reproductive site limitation should not cause
711 striking variations in the mating and reproductive success of males. Consequently, the overall
712 magnitude of the difference between values of opportunity for sexual selection in situations of
713 low and high reproductive site availability should be lower in temperate regions than in tropical
714 regions (Fig. 8B). This argument implies that detecting clear patterns of reproductive site
715 limitation on the opportunity for sexual selection is more difficult when we have a dataset that
716 is predominantly composed of species from temperate regions.

717



718

719 **Fig. 8.** Theoretical scheme illustrating the effect of climate seasonality on the degree of female
 720 monopolization, and thus on the intensity of sexual selection. (A) When climate seasonality is well-
 721 marked, the length of breeding season is short, leading to high synchrony in female reproduction. Due to
 722 synchronous female reproduction, the degree of female monopolization decreases, and the intensity of
 723 sexual selection follows the same trend. This scheme assumes an interaction between female reproductive
 724 synchrony and reproductive site limitation, so that when female reproduction is asynchronous the effect
 725 of reproductive site limitation is more pronounced than when female reproduction is synchronous. (B)
 726 The prediction is that the interaction between female reproductive synchrony and reproductive site
 727 limitation leads to a small overall effect size of the opportunity for sexual selection in temperate regions
 728 when compared to tropical regions.

729

730

731 The argument developed above reinforces the importance of the OSR, which represents
 732 how difficult is to find and secure a mating pair in the population (Kokko *et al.*, 2014). When
 733 female reproduction is asynchronous, reproductive site limitation is expected to have a more
 734 pronounced effect on the intensity of sexual selection than when female reproduction is
 735 synchronous because not only the reproductive sites are scarce, but there are few receptive
 736 females in the population (Fig. 8A). Thus, considering that the OSR varies both in time and
 737 space (e.g., Colwell & Oring, 1988; Gwynne, 1990; Pröhl, 2002; Forsgren *et al.*, 2004), the intensity
 738 of sexual selection may vary between populations and change over the course of the breeding

739 season even if the availability of reproductive sites is kept constant (e.g., Reichard *et al.*, 2008).
740 Consequently, if we want to achieve a deeper understanding of what factors drive differences in
741 the intensity of sexual selection in species with resource-based mating systems we should be
742 able to disentangle the social factor represented by the OSR from the ecological factor
743 represented by reproductive site limitation.

744

745 **3. Selection under male trait**

746 During the ongoing debate about how to measure the intensity of sexual selection, some
747 researchers advocated against the utility of the opportunity for sexual selection and proposed
748 that we need to focus on the selection gradient on species-specific traits that are under intra-
749 and/or intersexual selection, such as armaments and ornaments (e.g., Klug *et al.*, 2010a; Jennions
750 *et al.*, 2012). Other researchers, in turn, argued that the most indicated practice is to quantify
751 sexual selection using multiple approaches and build conclusions based both on direct
752 measures, such as selection gradients, and indirect measures, such as the opportunity for sexual
753 selection (e.g., Kelly, 2007; Fritzsche & Arnqvist, 2013; Cogliati *et al.*, 2014; Janicke *et al.*, 2016). In
754 the articles from our database, both direct and indirect measures of sexual selection have been
755 used and we analyzed them separately. Whereas the previous topic was devoted to the
756 opportunity for sexual selection, here we focus on the selection on male traits that are relevant
757 to reproductive site monopolization. Our results indicate that when reproductive sites are
758 limited, successful males (i.e., those that are able to monopolize a site and achieve copulations)
759 tend to have larger body size and armament size than unsuccessful males. Also, the slope of the
760 selection gradients on male traits tend to be steeper when reproductive sites are limited, which
761 means a stronger covariance between the size of a male trait and his mating or reproductive
762 success (Fig. 4). This finding indicates that sexual selection acting on male traits related to
763 resource monopolization is indeed stronger when reproductive sites are somehow limited.

764 Most of the studies included in our dataset focused on male body size, a trait that is usually
765 subject to intra- and inter-sexual selection (examples in Fairbairn *et al.*, 2007). According to our
766 results, when reproductive sites are limited, body size is a major determinant of male
767 reproductive success, probably because large males usually defeat small males in contests,
768 maintain the possession of the reproductive site, and thus have access to receptive females
769 (examples in Clutton-Brock, 1982 and Andersson, 1994). In several fish species, for instance, the
770 competition for reproductive sites is intense and only the largest males are able secure the
771 preferred sites, which may be rare in some natural populations (e.g., Lugli *et al.*, 1992; Forsgren
772 *et al.*, 1996; Mück *et al.*, 2013). Large males may also provide better parental care because they
773 are able to repel conspecific and heterospecific egg predators more efficiently (e.g., Townshend
774 & Wootton, 1985; Bisazza *et al.*, 1989; Lehtonen & Lindström, 2008). If reproductive site
775 limitation increases the risk of offspring predation in some species (see topic "5. Quality of
776 parental care" below), the sexual selection gradient on male size may be steeper because female
777 preference for larger males may provide higher direct benefits in terms offspring protection
778 (Price *et al.*, 1993; Kokko, 1998). Thus, both intra-sexual selection via male-male contests and
779 inter-sexual selection via female mate choice may favor large body sizes in situations of
780 reproductive site limitation.

781 In only a small number of species from our dataset males have structures used as
782 armaments, such as spines, hypertrophied claws, and enlarged mandibles (e.g., Debusse *et al.*,
783 2003; Kelly, 2007; Werneck, 2011). Although these armaments are mainly used in intrasexual
784 contests for reproductive site possession, they can also be target of female preference (Berglund
785 *et al.*, 1996; McCullough *et al.*, 2016). In fact, the mean effect size based on measures of body size
786 is higher than the mean effect size based on armament size (Fig. 7F), suggesting that armaments
787 had a smaller effect on male reproductive success when reproductive sites are somehow limited.
788 We highlight, however, that female preference for males bearing large armaments may have
789 some particular implications. Assuming that investment in armaments is usually costly, males

790 bearing exaggerated armaments may be better able to hold reproductive sites, but may have less
791 energy and time to invest in parental care (e.g., Forsgren, 1997; Qvarnström & Forsgren, 1998;
792 Wong & Candolin, 2005). This allocation trade-off may be particularly important for female mate
793 choice when males are the sole responsible for parental care, as occurs with several fish and
794 harvestman species in our dataset (Table 1). Moreover, the taxonomically widespread allocation
795 trade-off between armament size and testis size may render males bearing exaggerated
796 armaments better able to hold reproductive sites, but less efficient in sperm competition (e.g.,
797 Parker & Pizzari, 2010; Parker *et al.*, 2013). Thus, two interesting questions to be answered in
798 species with resource-based mating system and exclusive paternal care are: (1) Is the quality of
799 male care influenced by armament size? (2) Is paternity loss higher when males bear exaggerated
800 armaments?

801 Finally, there are three methodological aspects that deserve attention in future studies.
802 First, some studies provide selection gradients for several male traits, but most of these traits are
803 highly correlated with each other or with body size. This is a methodological issue that impacts
804 effect size calculation due to non-independence of the data (Nakagawa & Santos, 2012; Noble *et*
805 *al.*, 2017). If values of correlations between traits are provided, it is possible to include a
806 correlation matrix to control for the non-independence of the data in the meta-analyses. Second,
807 following the idea of evaluating several metrics to fully explore the intensity of sexual selection,
808 it would be useful to have selection gradients for traits that are mostly under pre-copulatory
809 selection, such as armaments and ornaments, and traits that are mostly under post-copulatory
810 selection, such as gonadal size and structures used in copulatory courtship. Thus, we can better
811 understand which traits have a greater contribution to the reproductive success of males in
812 places where reproductive sites are limited. Finally, in many studies it is not clear whether
813 females select the male or the nest site during mate choice (see discussion in Oliveira *et al.*, 2000
814 and Bose *et al.*, 2018). Although a positive correlation between male quality and nest site quality
815 is expected to occur, when nest sites vary in quality and are scarce, large males or males with

816 large armaments may be defending either high-quality or low-quality nests, which may insert
817 some noise in analyses of selection gradients. Thus, whenever possible, we should try to
818 understand what is the target of female mate choice to better explore how reproductive site
819 limitation may affect the intensity and direction of female preference.

820

821 **4. Sperm competition risk**

822 According to the theory, when reproductive sites are limited, the degree of female
823 monopolization is high, and non-territorial males should adopt opportunistic reproductive
824 behaviors to achieve copulations. Thus, males holding reproductive sites should experience high
825 sperm competition risk because many non-territorial males should sneak copulations inside or
826 around the reproductive sites (Gross, 1996; Oliveira *et al.*, 2008). In contrast with theoretical
827 expectations, our results show that reproductive site limitation has no clear effect on the overall
828 effect size of sperm competition risk (Fig. 5). However, we detected differences between mean
829 effect sizes when we examined different proxies of sperm competition risk. In situations of
830 reproductive site limitation, the frequency of males exhibiting ARTs and the frequency of EPCs
831 had no significant increase, but the gonadal investment of territorial males increased, and they
832 lost less paternity (see "Specific moderator" in Table 3 and Fig. 7G).

833 When reproductive sites are scarce, the territories defended by individual males are
834 usually far from each other, so that movements between reproductive sites by non-territorial
835 males should be more difficult (e.g., McLain, 1992; Almada *et al.*, 1994). For instance, males of
836 the harvestman *Serracutisoma proximum* have low vagility and when reproductive sites are far
837 from each other, some territories concentrate several sneakers, but others are not even found by
838 the sneakers. As a result, some territorial males experience high sperm competition risk, whereas
839 other males experience almost no risk (Muniz *et al.*, 2015). In turn, when reproductive sites are
840 abundant, the territories defended by individual males are usually close to each other and a

841 single male may invade several territories even if he is not very vagile (e.g., Jones *et al.*, 2001b,
842 Reichard *et al.*, 2004; Lehtonen & Lindström, 2008). In two fish species included in our dataset,
843 *Pimephales promelas* and *Pomatoschistus minutus*, both territorial and non-territorial males
844 may invade neighboring territories when reproductive sites are abundant and spatially clustered.
845 The same is not true when reproductive sites are scarce and spatially scattered, so that the
846 frequency of broods with illegitimate offspring is higher when site availability is high (Singer *et*
847 *al.*, 2006; Bessert *et al.*, 2007). Therefore, the spatial distribution of reproductive sites together
848 with the vagility of the study organisms may be more important than reproductive site limitation
849 to determine the rate of territory invasion, and consequently the sperm competition risk
850 experienced by territorial males.

851 A rationale similar to that presented above may also apply to EPCs in birds because
852 movements between distant territories are more difficult and risky for both territorial and non-
853 territorial males, as well as for females seeking for extra-pair partners. In this case, abundance
854 and proximity of reproductive sites may lead to higher density of breeding pairs, increasing the
855 chance of territory invasions and EPCs, which ultimately should increase sperm competition risk
856 and paternity loss. Although most of the individual effect sizes estimated for birds are negative,
857 there is great variation and most of the confidence intervals cross zero (Fig. 5). This result
858 indicates that sperm competition risk is not consistently higher in populations where
859 reproductive sites are abundant and probably spatially close to each other. In fact, an extensive
860 review of the literature shows that there is little evidence for a consistent relationship between
861 breeding density and percentage of extra-pair paternity in intraspecific studies with birds
862 (reviewed in Griffith *et al.*, 2002).

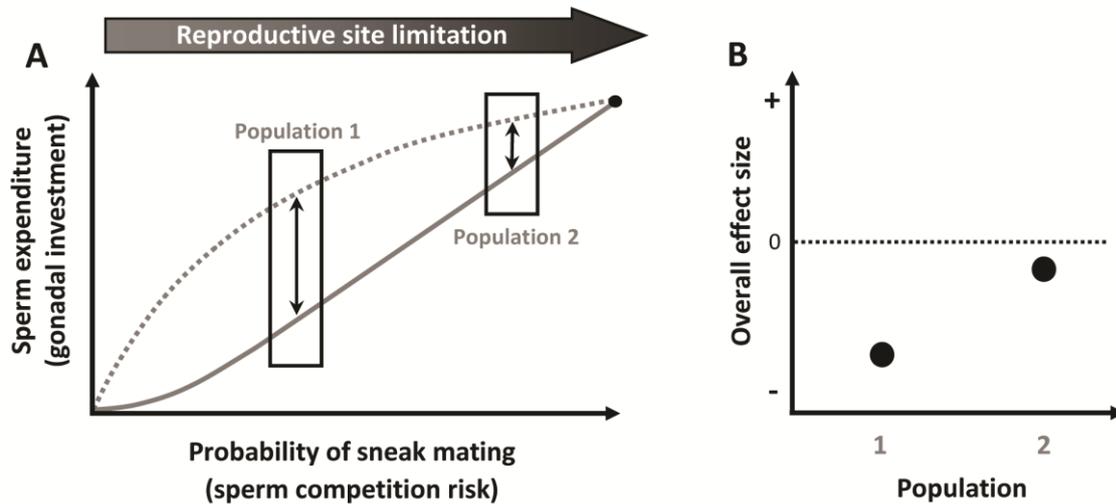
863 According to theoretical models, territorial males should increase their gonadal
864 investment when sperm competition risk increases (Parker, 1990; Fig. 9A). Our results indicate
865 that territorial males have higher gonadal investment when reproductive sites are somehow
866 limited (Table 3, Fig. 7G). It is important to emphasize that all effect sizes about gonadal

867 investment were calculated from studies conducted with fish exhibiting ARTs (see online
868 Appendix 2). Thus, although the frequency of males exhibiting ARTs was not affected by
869 reproductive site limitation, territorial males of several fish species seem to be responding
870 plastically to an increase in sperm competition when reproductive sites are somehow limited.
871 Probably, the environmental cue that are triggering the increase in gonadal investment by
872 territorial males is not the frequency of males exhibiting ARTs in the population, as assumed in
873 several empirical studies on sperm competition (see discussion in Ota *et al.*, 2010 and Munguía-
874 Steyer *et al.*, 2012). We suggest that territorial males may be able to perceive other social cues of
875 sperm competition risk, such as the rate of fights with conspecific males, which seems to respond
876 to reproductive site limitation as we discussed before.

877 Assuming that reproductive site limitation indeed increases the probability of sneak and
878 furtive mating, theoretical models indicate that the maximum difference in gonadal investment
879 between territorial and sneakers occurs at intermediate levels of sperm competition risk (Parker,
880 1990; Fig. 9A). As the sperm competition risk increases, the difference in gonadal investment
881 between territorial and sneakers decreases (Parker, 1990; Fig. 9A). Therefore, when reproductive
882 sites are not limited, the probability of sneak mating is not very high, and the gonadal
883 investment of territorial males is much lower than the gonadal investment of sneaker males. In
884 this case, if a sneak fertilization occurs, the paternity loss of territorial males should be high (Fig.
885 9A-B). In turn, when reproductive sites are somehow limited, the probability of sneak mating is
886 high, and the gonadal investment of territorial and sneaker males are more similar. Thus,
887 territorial males should secure more offspring paternity (Fig. 9A-B). We argue that this
888 framework could explain why paternity loss in our dataset followed the same pattern in most
889 fish and bird species, and showed lower values when reproductive sites are somehow limited
890 (i.e., the mean effect size was negative, Fig. 7G). Although more complex than our initial
891 prediction (Table 2), the framework based on theoretical models of sperm competition (Fig. 9)

892 seems to provide more realistic predictions and a better fit with the empirical data we gathered
893 here.

894



895

896 **Fig. 9.** (A) Scheme illustrating the effect of sperm competition risk on the gonadal investment of territorial
897 males (solid line) and sneaker males (dotted line) according to the theoretical model by Parker (1990).
898 The greatest difference in the gonadal investment between territorial and sneaker males occurs at
899 intermediate levels of sperm competition risk (Population 1), which is assumed to covary with
900 reproductive site limitation. When reproductive sites are limited, and the sperm competition risk is high,
901 the difference in the gonadal investment of territorial and sneaker males is small (Population 2). (B) The
902 difference in gonadal investment of territorial and sneaker males may influence paternity loss of territorial
903 males. Under low reproductive site limitation, sneaker males produce better-quality or more sperm than
904 territorial males, so that paternity loss of territorial males should be high (Population 1). In turn, under
905 high reproductive site limitation, sneaker and territorial males produce similar quality or quantity of
906 sperm, so that paternity loss of the territorial males should be low (Population 2). According to the way
907 we calculated effect sizes (subtracting paternity loss under low from the paternity loss under high
908 reproductive site limitation), negative effect sizes indicate that territorial males are losing less paternity
909 when reproductive site are more limited (i.e., Population 2).

910

911 5. Quality of paternal care

912 According to the life-history theory, each individual has a limited amount of time and energy to
913 invest in different activities or body structures, so that allocation trade-offs are expected to
914 emerge between different fitness components (Stearns, 1989). Thus, when reproductive sites are
915 limited, males should expend more time and energy on male-male competition, leading to a
916 decrease in the quality of paternal care. Contrary to this theoretical prediction, we found a small
917 and positive overall effect size, which means that the quality of paternal care is slightly higher
918 when reproductive sites are somehow limited. However, the confidence interval of the overall
919 effect size crossed zero, suggesting that there is no clear trend in the dataset (Fig. 6). Moreover,
920 measures of effect size related to costs paid by the offspring and costs paid by parental males do
921 not show any significant difference (Table 3). However, the effect of reproductive site limitation
922 on the quality of paternal care has been poorly studied in the literature of mating systems, and
923 our dataset includes only 19 effect sizes (Fig. 6). We argue that this trend may be partially
924 explained by the fact that clear predictions on the effect of reproductive site limitation on the
925 quality of paternal care depend on details of the natural history of each species, as well as on
926 other ecological conditions. The combination of several different factors certainly hampers
927 generalizations.

928 As should be expected by the theory, in some fish species with exclusive male care, there
929 is an allocation trade-off between reproductive site defense and parental activities, such as egg
930 fanning and egg cleaning (e.g., Oliveira *et al.*, 2000; Lehtonen & Lindström, 2008; but see
931 Pizzolon *et al.*, 2012). However, in many fish species (and also some invertebrates), allocation
932 trade-offs may not necessarily occur because parental activities can be aligned with reproductive
933 site defense. For instance, if the main function of the males in species with exclusive paternal
934 care is to prevent egg predation, nest defense and egg protection are not concurrent activities.
935 In this case, no allocation trade-off is expected to emerge because the more fiercely a male
936 defends his nest, the better should be the protection provided to the eggs inside the nest. In fact,

937 in several fish species in which the quality of parental care increased under reproductive site
938 limitation (i.e., positive effect sizes in Fig. 6), the variables that generated the effect sizes were
939 related to the time parental males spent close or inside their nests and to the frequency of
940 chasings against potential egg predators (e.g., Townshend & Wootton, 1985; Lehtonen &
941 Lindström, 2008; Saraiva *et al.*, 2009, 2012).

942 In birds with biparental care, an increase in agonistic interactions for the possession of
943 reproductive sites may also lead to a decrease in food provisioning for the chicks by males (e.g.,
944 Jacot *et al.*, 2009). However, a higher male investment in agonistic interactions for the
945 possession of the reproductive site may be compensated by an increase in female investment in
946 egg incubation and food provisioning for the chicks (e.g., Hinde, 2005; Jacot *et al.*, 2009). Thus,
947 although there is a clear mechanistic connecting the reproductive site limitation and the quality
948 of paternal care, studies that compare offspring performance between populations with low and
949 high reproductive site limitation may find no pattern (e.g., Jacot *et al.*, 2009). Other important
950 aspect to be considered in observational field studies conducted with biparental species is that
951 other ecological conditions, rather than reproductive site limitation, may affect the quality of
952 parental care, and thus offspring performance. Two possible ecological conditions are predation
953 intensity and food availability. When predation pressure is intense, males should be less prone
954 to exit the nest and, food provisioning for the chicks should be low regardless of reproductive
955 site limitation (e.g., Dale *et al.*, 1996; Ghalambor & Martin, 2000). When food availability is high,
956 males should decrease their parental effort and increase their mating effort, so that food
957 provisioning for the chicks should be performed mostly by females, regardless of reproductive
958 site limitation (e.g., Markman *et al.*, 1995; Harding *et al.*, 2004). Thus, future field studies with
959 birds should try to disentangle the effects of reproductive site availability from others
960 confounding effects, such as predation intensity and food availability, using a controlled
961 experimental approach.

962 Based on the arguments and examples presented above, idiosyncratic responses of species
963 showing either exclusive paternal care or biparental care should lead to no general trend in meta-
964 analytic studies, and to a great importance of species identity in explaining the variance in the
965 data. These two results were exactly what we found here. We argue that, if we want to
966 understand the effects of reproductive site limitation on the quality of paternal care, other
967 aspects should be taken into account, including the main function of the males for the offspring
968 survival, the possibility of female compensation of parental care, and other environmental
969 factors that may concomitantly affect the quality of paternal care.

970

971 **V. CONCLUSION**

972 (1) When reproductive sites are limited, males respond with a small increase in competition.
973 Given that the possession of a reproductive site is crucial for males in species with resource-
974 based mating systems, the small magnitude of the effect we found here was unexpected. We
975 argue that male-male competition may be attenuated by: (i) the establishment of dominance
976 hierarchies among males, which decreases physical combats between low-ranking and high-
977 ranking males; (ii) plasticity in male mating tactics, so that each male may act either as territorial
978 or sneaker depending on the availability of reproductive sites; and (iii) flexibility in the use of
979 reproductive sites by female, which may decrease the importance of holding the most valuable
980 sites for the reproductive success of males.

981 (2) Reproductive site limitation has no consistent effect on the opportunity for sexual selection.
982 Apparently, the effect of extra-pair copulations and sneak copulations on the variance in male
983 reproductive success is not consistent across species, so that the opportunity for sexual selection
984 may either increase or decrease. Moreover, our dataset has a bias for species from temperate
985 regions, which usually have short breeding seasons with high synchrony in female reproduction.
986 We argue that the low potential for female monopolization due to reproductive synchrony leads

987 to low variance in male reproductive success. Thus, the effect of reproductive site limitation on
988 the intensity of sexual selection should be lower in temperate than in tropical species.

989 (3) When reproductive sites are limited, there is a small increase in the selection gradient
990 favoring male traits that increase resource monopolization, such as body size. Larger males tend
991 to win fights for the possession of scarce reproductive sites and achieve more copulations than
992 smaller males. Besides intrasexual selection via male-male competition, intersexual selection via
993 female mate choice may also favor larger males if they provide better care for the offspring, as
994 occurs with several fish species.

995 (4) Reproductive site limitation has no consistent effect on sperm competition risk. However,
996 territorial males invest more in gonads and lose less paternity when reproductive sites are
997 limited. We suggest that males respond plastically to social cues, such as an increase in the rate
998 of territorial fights, and increase their gonadal investment following classic theoretical models
999 of sperm competition risk. Assuming that the difference in gonadal investment between
1000 territorial and sneaker males decreases as reproductive site limitation increases, territorial males
1001 should lose less offspring due to sperm competition, which is in accordance with our results.

1002 (5) There is no clear effect of reproductive site limitation on the quality of paternal care, but few
1003 empirical studies have addressed this subject. Whereas the quality of paternal care decreased as
1004 reproductive site limitation increases, the opposite pattern was also found for some species. We
1005 argue that the theoretical trade-off between paternal care and reproductive site defense should
1006 be attenuated if the main function of the males is to prevent egg predation, because nest defense
1007 and egg protection are not concurrent activities. Moreover, ecological factors, such as predation
1008 intensity and food availability, may be more important than reproductive site limitation in
1009 determining the quality of parental care, and thus offspring survival.

1010 (6) Taken together, our findings indicate that predictions on how reproductive site limitation
1011 may affect the organizations of resource-based mating systems have weak empirical support,

1012 even in laboratory experiments in which possible confounding effects are controlled. These
1013 predictions, which are directly or indirectly based on the mating system theory, do not consider
1014 the plasticity in the mating tactics of males and females, which make them too simplistic.
1015 Moreover, since the original proposition of the mating system theory, our understanding of
1016 sperm competition increased a lot. We now know that more accurate predictions on the
1017 intensity and direction of sexual selection should take into account both pre- and post-
1018 copulatory processes. Finally, the interplay between sexual selection and parental care is
1019 complex, and the original framework of mating system theory does not provide sufficient
1020 elements to derive clear and taxonomically broad predictions.

1021

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1366 **VIII. SUPPORTING INFORMATION**

1367

1368 **Appendix 1:** Table S1. List of terms used in the literature search; Fig. S1. PRISMA flow diagram;
1369 Table S2. Article excluded from the analyses.; Fig. S2. Phylogenetic tree of the species included
1370 in the meta-analyses; Fig. S3. Funnel plots for predictions 1-5; Table S3. Results of Egger's test for
1371 predictions 1-5; References.

1372

1373 **Appendix 2.** All files necessary to reproduce our analyses. For each prediction we provide: (i) a
1374 *.csv* file with the data input; (ii) a *.tre* file with the phylogenetic tree; (iii) a *.Rmd* file with the
1375 commented code; and (iv) a *.html* file produced with RMarkdown, in which is possible visualize
1376 the full analyses, with the code, graphs and results. These files can be downloaded in the
1377 following address:

1378 <https://www.dropbox.com/sh/wbbs8v4aincq42f/AAAlv-ucYoojNGMjntcedoiSa?dl=0>.

1379

1380

APPENDIX 1

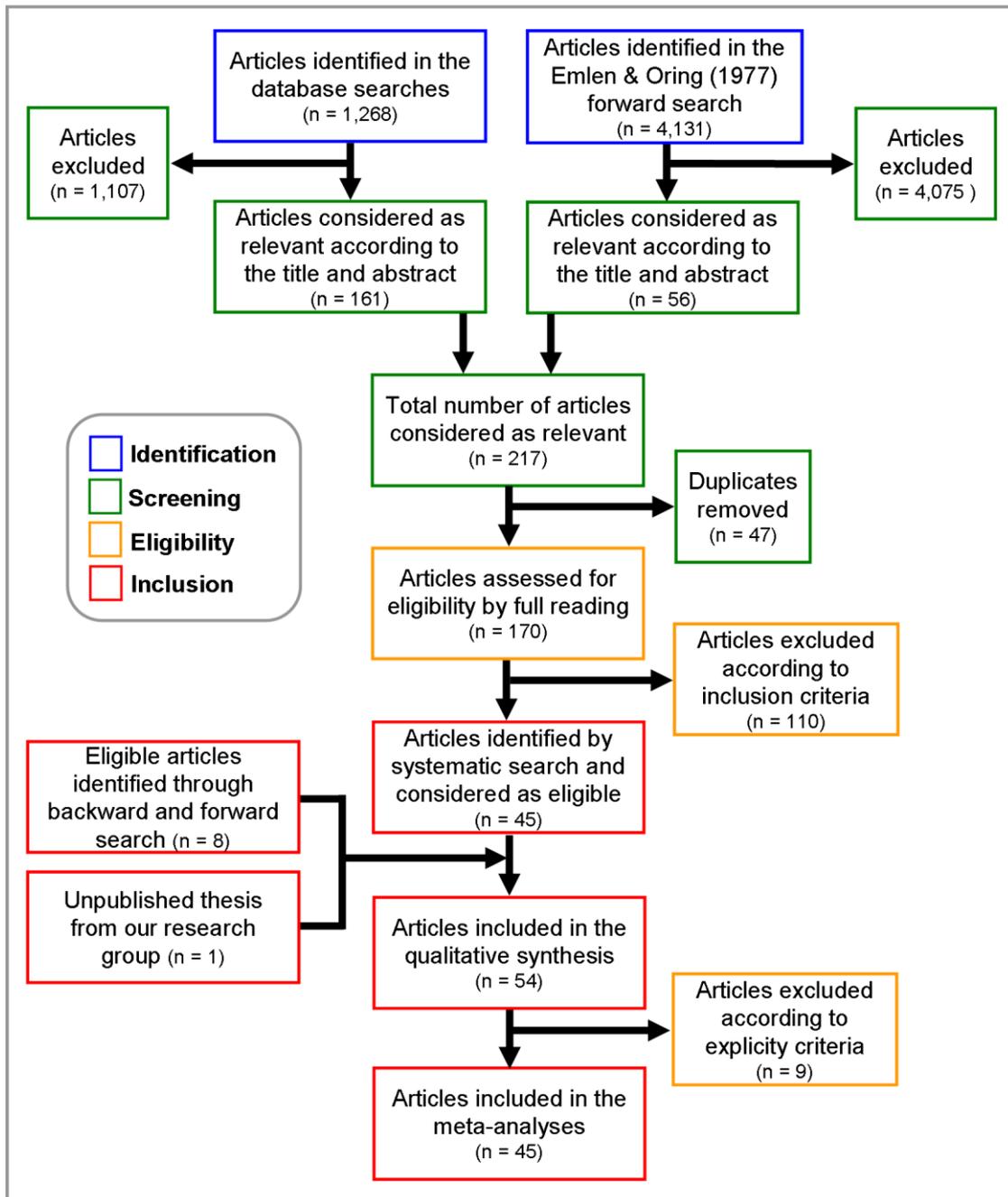
1381

1382 **Table S1.** List of terms used in the literature search conducted in two data bases: *Web of*
 1383 *Science* and *Google Scholar*. In both data bases, the search included all articles published
 1384 between 1977 and March 2018.

1385

Data base	Search terms
<i>Web of Science</i>	("resource availab*" OR "spatial distribution" OR "resource limitation") AND "mating system"
<i>Web of Science</i>	("availability" OR "density" OR "limitation") near/5 (resource OR nest OR site) AND "mating system"
<i>Web of Science</i>	("natural cavit*" OR shelter OR "nest box" OR burrow OR "tree hole" OR "empty shell*" OR "hollow tree") AND "mating system"
<i>Web of Science</i>	("territory availab*" OR "territory limitation") AND "mating system"
<i>Web of Science</i>	("breed* site" OR "nest* site" OR "reproduct* site" OR nest) near/5 (limitation OR availability OR restriction) AND ("parental care" OR "maternal care" OR "paternal care")
<i>Google Scholar</i>	"resource quality" OR "resource availability" OR "resource distribution" OR "resource limitation" "mating system" -food -plant
<i>Google Scholar</i>	Emlen & Oring (1977) forward search

1386



1387

1388 **Fig. S1.** PRISMA flow diagram detailing each step of the literature search: (1) studies
 1389 identification by data base searching and by forward searching of the paper by Emlen & Oring
 1390 (1977); (2) selection of relevant studies by screening the title and abstract of each article;
 1391 full-reading of relevant articles, assessing the eligibility criteria detailed in the main text, and
 1392 including new studies identified by backward and forward search; (4) exclusion of some articles
 1393 that do not math some inclusion criteria (see Table S2), but that were considered as relevant for
 1394 the qualitative analysis (see Table 2 in the main text). After these four steps, we defined the final
 1395 dataset for the meta-analyses.

1396

1397 **Table S2.** Reasons for the exclusion of some articles included in the qualitative synthesis but
 1398 excluded from the meta-analyses.

1399

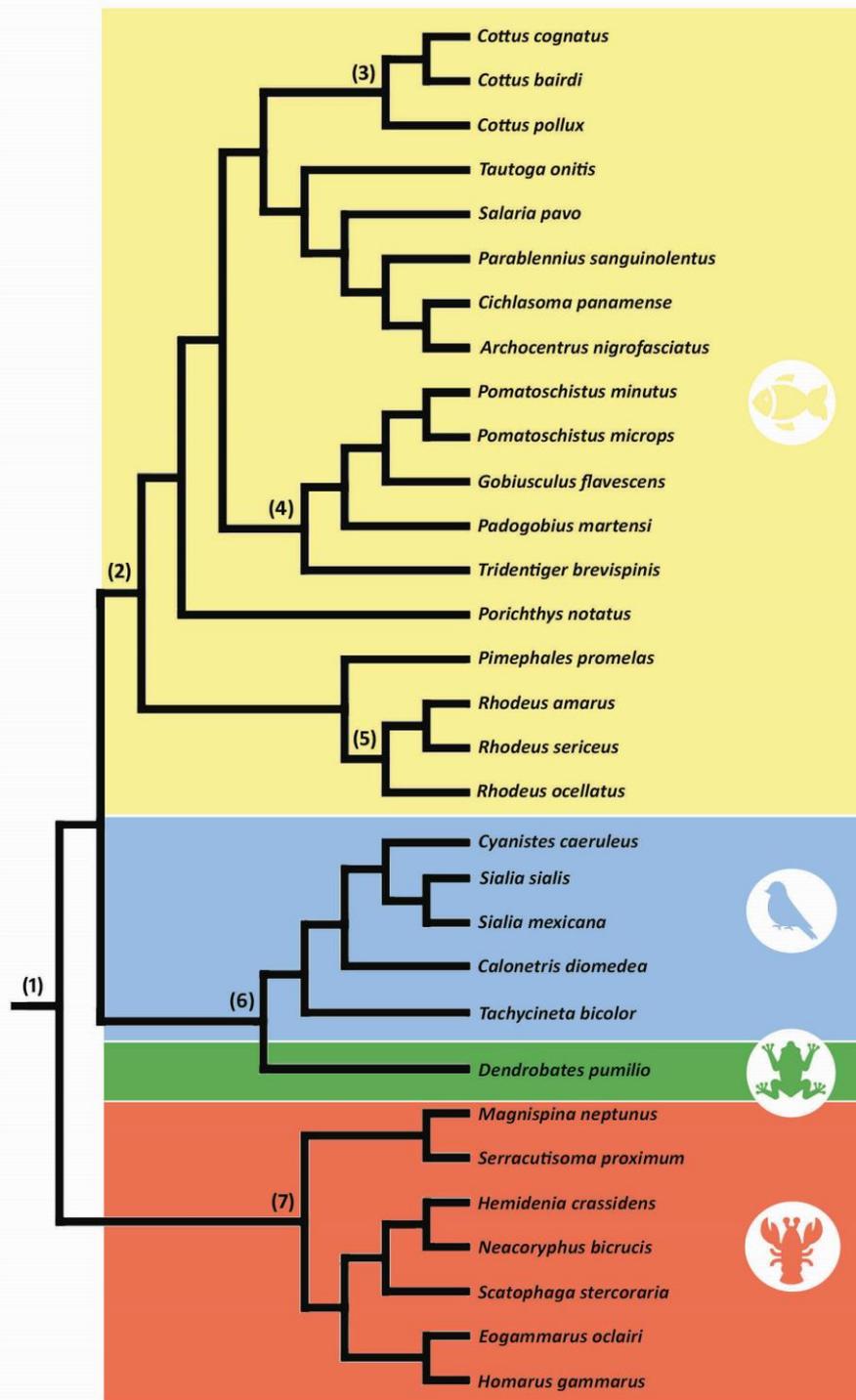
Reference	Reason of exclusion
Almada <i>et al.</i> , 1994	The article provides information only on the area/population with high nest site limitation.
Bried <i>et al.</i> , 2010	The article provides information on one population and compares the data with other populations studied by other authors. However, the methods used in different studies are not comparable.
Cleveland-Roberts & Itzkowitz, 2009	Nest site limitation is not the focus of the experiment and the authors do not manipulate this factor.
Lindström & Seppa, 1996	The article provides information on the number of mates, but only for the males who mated. This is a problem to calculate the opportunity for sexual selection (I), because this index should take into account the unsuccessful males.
Maan & Taborsky, 2008	The authors manipulated the number of eggs and paternity in shells (nest sites) and measured the frequency of turnovers and nest takeovers. However, there is no treatment of nest site limitation.
McLain, 1992	The article provides information on fluctuations of resource availability, but there is no treatment of reproductive site limitation. Moreover, there is no information on the number of males or population density, which hampers the identification of conditions of low and high nest site limitation.
Olla <i>et al.</i> , 1981	The experiment was not focused on testing the influence of nest limitation. Moreover, the authors varied the number of males, females, and nest at the same time. Finally, it was impossible to extract information from the graphics.
Sato, 1994	The study was conducted in only one population where the authors investigated the use of different types of shell by the study species.
Wong <i>et al.</i> , 2008	The authors manipulated the number of nest sites, but the data presented in the article is focused only on female behavior.

1400

1401 **Assembly of phylogenetic tree used in the meta-analyses**

1402 Given that no phylogenetic study published so far comprises all species included in our dataset,
1403 we assembled different phylogenies to obtain the super-tree presented in Figure S2. This super-
1404 tree includes 31 species belonging to the following major groups: (1) Actinopterygii (fish), (2)
1405 Aves (birds), (3) Anurans (frogs), and (4) Arthropoda (arachnids, crustaceans, and insects). The
1406 backbone of the super-tree (node 1) is based on Blair & Hedges (2005). The relationship of the
1407 major fish clades (node 2) is based on Betancur *et al.* (2013). The internal phylogeny of the family
1408 Gobiidae (node 4) is based on Thacker & Roje (2011), and the internal phylogenies of the genera
1409 *Cottus* (node 3) and *Rhodeus* (node 5) are based on Yokoyama & Goto (2005) and Bohlen *et al.*
1410 (2006), respectively. The relationship of the major bird clades (node 6) is based on Jønsson &
1411 Fjeldså (2006) and Prum *et al.* (2015). Finally, the relationship of the major arthropod clades
1412 (node 7) is based on Ishiwata *et al.* (2010) and Rota-Stabelli *et al.* (2012).

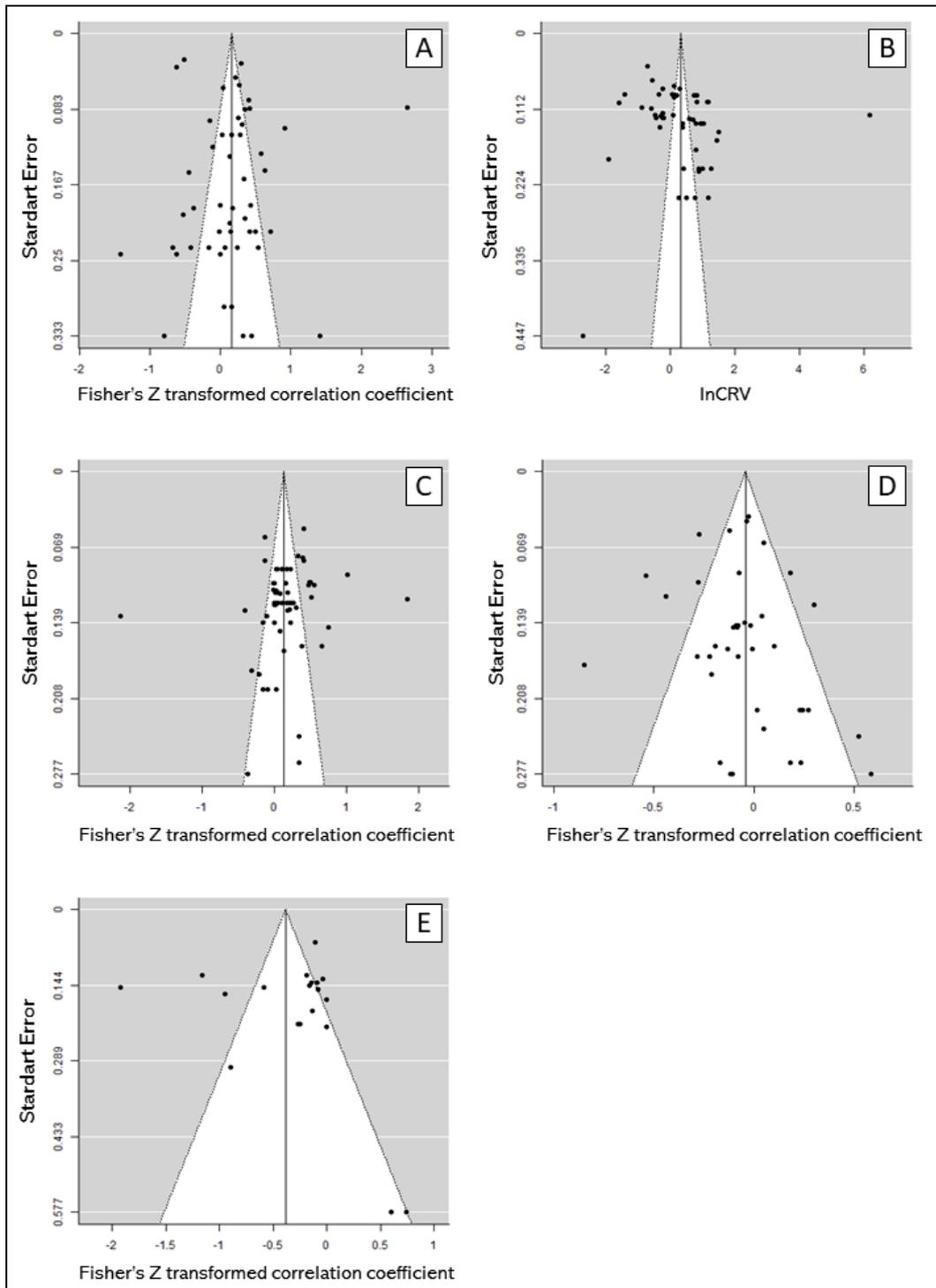
1413



1414

1415 **Fig. S2.** Phylogenetic tree showing the evolutionary relationship between the species included
 1416 in the meta-analyses. The tree was constructed in the software *Mesquite* (Maddison & Maddison,
 1417 2018).

1418



1419

1420 **Fig. S3.** Funnel plots for predictions 1 (A), 2 (B), 3 (C), 4 (D), and 5 (E). Each point represents the
 1421 value of an effect size and its respective standard error. The white triangle represents the range
 1422 of values where 95% of the data points would lie in the absence of publication bias. If the shape
 1423 of the funnel is symmetrical, this suggests absence of publication bias. The vertical line
 1424 represents the value of mean effect size estimated by each meta-analytic model.

1425

1426 **Table S3.** Results of Egger's test for predictions 1-5. This test indicates possible publication bias
 1427 for a significant difference between the dataset intercept and zero. Values of $p < 0.05$ indicate
 1428 possible publication bias. d.f. = degrees of freedom, s.e. = standard error.
 1429

Prediction	d.f.	p	Parameter	Estimate	s.e.	t-value	p
P1	49	0.348	Intercept	2.270	1.415	1.604	0.115
			Precision	-0.123	0.130	-0.948	0.348
P2	46	0.132	Intercept	7.561	3.884	1.947	0.057
			Precision	-0.662	0.432	-1.531	0.132
P3	67	0.027	Intercept	-1.907	1.471	-1.297	0.199
			Precision	0.336	0.162	2.251	0.027
P4	39	0.059	Intercept	0.330	0.535	0.616	0.541
			Precision	-0.111	0.057	-1.944	0.059
P5	17	0.812	Intercept	1.977	2.179	0.907	0.377
			Precision	-0.075	0.314	-0.241	0.813

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