



**UNIVERSIDADE FEDERAL DE GOIÁS**  
**INSTITUTO DE CIÊNCIAS BIOLÓGICAS**  
**PROGRAMA DE PÓS-GRADUAÇÃO EM ECOLOGIA E EVOLUÇÃO**



**COMO O COMPORTAMENTO ANIMAL PODE INFLUENCIAR A DISTRIBUIÇÃO  
DAS ESPÉCIES**

**Herlander Correia de Lima**

**Orientador: Thiago Fernando Rangel**

**Co-orientador: Diogo Soares Menezes Samia**

**Goiânia**

**Março 2018**

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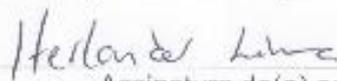
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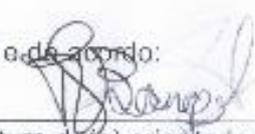
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*Dissertação apresentada à Universidade Federal de Goiás  
como parte das exigências do Programa de Pós-graduação  
em Ecologia e Evolução para obtenção do título de Mestre  
em Ecologia e Evolução*

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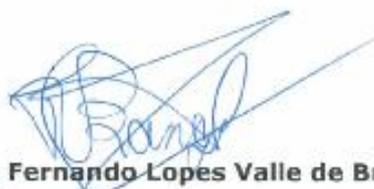


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**ATA DA SESSÃO PÚBLICA DE DEFESA DE DISSERTAÇÃO DE Nº 159**

Aos vinte e um dias do mês de março de dois mil e dezoito (21/03/2018), às quatorze horas (14h), no Auditório o ICB V - Campus Samambaia - UFG, reuniram-se os componentes da banca examinadora: **Prof. Dr. Thiago Fernando Lopes Valle de Britto Rangel, ICB-UFG; Prof. Dr. Fausto Nomura, ICB-UFG; Dr. Jean Carlos Gonçalves Ortega, UEM-PR;** para, em sessão pública presidida pelo primeiro examinador citado, procederem à avaliação da defesa de dissertação intitulada: "**Como o comportamento animal pode influenciar a distribuição das espécies**", em nível de mestrado, área de concentração em Ecologia e Evolução, de autoria de **Herlander Correia de Lima**, discente do Programa de Pós-Graduação em Ecologia e Evolução da Universidade Federal de Goiás. A sessão foi aberta pelo presidente, que fez a apresentação formal dos membros da banca. A palavra, a seguir, foi concedida à(o) autor(a) da dissertação que, em cerca de 30 minutos, procedeu à apresentação de seu trabalho. Terminada a apresentação, cada membro da banca arguiu à(o) examinada(o), tendo-se adotado o sistema de diálogo sequencial. Terminada a fase de arguição, procedeu-se à avaliação da dissertação. Tendo-se em vista o que consta na Resolução nº 1127 de dezembro de 2012 do Conselho de Ensino, Pesquisa, Extensão e Cultura (CEPEC), que regulamenta o Programa de Pós-Graduação em Ecologia e Evolução, a dissertação foi Aprovado, considerando-se integralmente cumprido este requisito para fins de obtenção do título de Mestre em Ecologia e Evolução pela Universidade Federal de Goiás. A conclusão do curso dar-se-á quando da entrega da versão definitiva da dissertação na secretaria do programa, com as devidas correções sugeridas pela banca examinadora, no prazo de trinta dias a contar da data da defesa. Cumpridas as formalidades de pauta, às 16 h e 05 min., encerrou-se a sessão de defesa e, para constar, eu, Suely

Ana Ribeiro, secretária executiva da Universidade Federal de Goiás - UFG, lavrei a presente ata que, após lida e aprovada, será assinada pelos membros da banca examinadora em três vias de igual teor.



**Prof. Dr. Thiago Fernando Lopes Valle de Britto Rangel**  
**Presidente da Banca**  
**ICB-UFG**



**Prof. Dr. Fausto Nomura**  
**ICB/UFG**

*Jean Carlos Gonçalves Ortega*  
**Dr. Jean Carlos Gonçalves Ortega**  
**UEM-PR**



*Dr. Diego Soares Moraes Sousa*  
**USP-SP**

*“Where the determination is, the way can be found.”*

Dabasir em “Richest Man in Babylon”

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# 1 INTRODUÇÃO GERAL

2 A forma como nos comportamos influencia não só nossas vidas, como também o mundo à nossa  
3 volta. Todas as pessoas apresentam diferenças de comportamento consistentes, que nos permitem  
4 muitas vezes predizer as decisões que irão tomar frente a determinadas situações. Por exemplo,  
5 diferenças de comportamento podem predizer a motivação de uma pessoa para migrar a outra  
6 região, tendo um papel tão importante nos fluxos de migração, que levou à criação do conceito de  
7 ‘personalidade do migrante’ (Tabor et al. 2015). Estudos têm demonstrado que pessoas mais  
8 extrovertidas, mais abertas a novas experiências, e mais individualistas são mais propensas a  
9 abandonar o seu território em busca de novas oportunidades (Camperio Ciani et al. 2007, Jokela  
10 2009, Otto and Dalbert 2012). Alguns estudos encontraram ainda uma relação entre o alelo DRD4  
11 (ligado à atração por novas experiências) e a expansão global humana nos tempos pré-históricos  
12 (Chen et al. 1999, Matthews and Butler 2011). Assim, na nossa espécie, indivíduos que abandonam  
13 território familiar não são uma amostra aleatória da população residente, dado que diferenças  
14 comportamentais podem ser um dos meios impulsionadores da decisão de partida.

15 As conclusões sobre a influência do comportamento humano nas dinâmicas de migração podem  
16 ser semelhantes para as espécies de animais não-humanos. Contudo, muitos cientistas têm mostrado  
17 relutância em aceitar que emoções, traços comportamentais, e capacidades cognitivas humanas  
18 podem apresentar semelhanças com outros animais, embora sejam amplamente aceitas tais  
19 semelhanças em relação aos caracteres fisiológicos ou morfológicos (Gosling and John 1999). Isto é  
20 inesperado, dado que nada em teoria evolutiva aponta para uma descontinuidade entre humanos e  
21 animais relativa a comportamento, nem tampouco que o comportamento é isento de pressões  
22 seletivas (Gosling and John 1999). Charles Darwin publicou em 1872 um livro intitulado “A  
23 expressão de emoções em humanos e animais” descrevendo similaridades entre o comportamento  
24 humano e outros animais (Shivik 2017). Dez anos depois, o biólogo evolutivo e fisiologista George  
25 Romanes afirma em seu livro “Inteligência animal” que mesmo espécies muito diferentes de

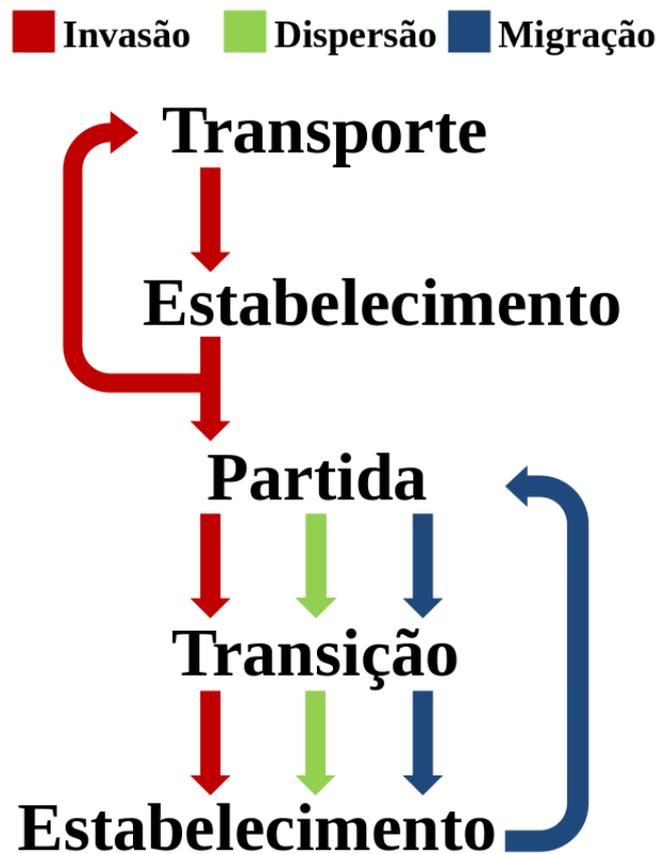
26 humanos podem possuir emoções como medo, curiosidade e carinho (Shivik 2017). Contudo, o  
27 comportamento animal era visto como ciência especulativa e subjetiva e, por vários anos, cientistas  
28 preferiram adotar métodos que permitiam maior rigor de medição e maior comparabilidade, como é  
29 o caso de traços morfológicos. Apenas em meados do século XX pesquisadores começaram a  
30 mostrar interesse em desenvolver métodos para o estudo das diferenças comportamentais em  
31 animais. Conseqüentemente, com o desenrolar dos anos, inúmeros estudos têm reportado a  
32 existência de diferenças de comportamento entre indivíduos, consistentes ao longo do tempo e  
33 sobre diferentes contextos, ao que se tem dado o nome de ‘personalidade animal’ (Carere and  
34 Maestripieri 2013). Estas diferenças comportamentais podem ser governadas por mecanismos  
35 fisiológicos (Grootuis et al. 2008), genéticos (Dochtermann et al. 2014), epigenéticos (Verhulst et  
36 al. 2016) e hereditários (Oers et al. 2004).

37 Nos dias de hoje, um dos grandes desafios no estudo do comportamento animal é entender se  
38 diferenças comportamentais podem levar a diferentes vantagens adaptativas e contribuir para a  
39 explicação de padrões ecológicos e evolutivos. Estudos já revelaram que diferenças  
40 comportamentais podem influenciar a atividade reprodutiva (Ariyomo and Watt 2012),  
41 vulnerabilidade à predação (Sih et al. 2003), parasitismo (Seaman and Briffa 2015), seleção sexual  
42 (Schuett et al. 2011), desempenho (Smith and Blumstein 2008), entre outros (revisado em Wolf and  
43 Weissing 2012). Isto sugere que a fixação de diferenças comportamentais nas populações resulta  
44 das inerentes vantagens ou desvantagens de cada tipo de comportamento em determinado contexto  
45 ecológico-evolutivo. Por exemplo, Riechert and Hall (2000) demonstraram que indivíduos de uma  
46 espécie de aranha vivendo em áreas com elevado risco de predação eram mais tímidos que  
47 indivíduos em áreas de menor risco predatório e menor abundância de recursos. Transplantes  
48 recíprocos de indivíduos entre as duas áreas resultaram em elevada mortalidade e baixa taxa de  
49 crescimento populacional, tornando evidente que certos traços comportamentais podem determinar  
50 vantagens competitivas consoante as condições ecológicas e/ou ambientais do meio. Neste sentido,

51 espécies que possuem elevada variação comportamental podem ser mais capazes de sobreviver a  
52 perturbações no meio, que espécies com baixa variação comportamental (Sih et al. 2012).

53 Tais perturbações são cada vez mais frequentes devido às consequências das mudanças globais na  
54 biodiversidade (Chapin III et al. 2000, Dirzo et al. 2014). Frente às mudanças ambientais, os  
55 animais possuem geralmente duas opções: dispersar ou adaptar-se por meio de plasticidade  
56 fenotípica ou mudanças genéticas (Williams et al. 2008, Wong and Candolin 2015). Um agravante é  
57 que mudanças provocadas pelo homem são geralmente tão rápidas que processos evolutivos  
58 dificilmente poderão garantir a persistência de muitas das espécies (Chevin and Lande 2010).  
59 Assim, para espécies que não possuem variação fenotípica na população que lhes permita tolerar as  
60 novas condições, a capacidade de dispersar torna-se um atributo vital. Por isso, entender as  
61 motivações para o abandono de um território, e como os indivíduos conseguem sobreviver durante  
62 a transição e o estabelecimento em novos meios é fundamental para conhecer que espécies estão  
63 mais aptas a resistir aos novos desafios.

64 Num contexto biogeográfico, os indivíduos podem dispersar e estabelecer-se com sucesso em  
65 outro meio através de três processos: a dispersão, a migração ou invasão. Apesar de existirem  
66 diferenças importantes entre estes processos, todos eles englobam os estágios de partida, transição e  
67 estabelecimento (Figura 1) (Clobert et al 2009, Blackburn et al. 2011, Chapman et al. 2011a).  
68 Vários traços como condição corporal (Lopez et al. 2012), sucesso reprodutivo (Duckworth 2008) e  
69 comportamento (Liebl and Martin 2012) são tidos como importantes para o sucesso dos indivíduos



**Figura 1** – Diagrama dos estágios de expansão de território nos processos biogeográficos de invasão (fluxo vermelho), dispersão (fluxo verde) e migração (fluxo azul)

70 na expansão do território (Chuang and Peterson 2016). Do ponto de vista comportamental,  
 71 indivíduos que possuam tipos de comportamento que lhes permitam motivar a decisão de partida e  
 72 assistir na transição e estabelecimento, podem ser os principais responsáveis pela expansão de  
 73 território (Canestrelli et al. 2016). Deste modo, diversas revisões narrativas têm procurado explicar  
 74 como as diferenças de comportamento podem influenciar a expansão do território (Cote et al.  
 75 2010a, Chapman et al. 2011a, Chapple et al. 2012, Wolf and Weissing 2012, Canestrelli et al. 2016).  
 76 Contudo, ainda é necessário um tratamento sistemático da literatura disponível e suporte empírico  
 77 para distinguir os padrões gerais dos casos específicos ou relações espúrias. Diante disso, o  
 78 Capítulo 1 deste trabalho recorre a uma revisão sistemática e meta-análise para avaliar se diferenças  
 79 comportamentais podem influenciar a capacidade de expansão do território. Os resultados  
 80 mostraram que os indivíduos que motivam a expansão de território podem apresentar diferenças de

81 comportamento face aos que não abandonam o território, potencialmente criando uma distribuição  
82 não-aleatória das espécies e/ou populações consoante tipos comportamentais. A expansão do  
83 território é sobretudo motivada por indivíduos com um comportamento mais exploratório e mais  
84 ousado. Ao analisar se os resultados podiam divergir para os distintos processos biogeográficos,  
85 demonstrei também que os indivíduos dispersores são mais exploratórios e ousados que não  
86 dispersores, e que invasores são mais ativos e mais exploratórios que nativos. Entretanto, o baixo  
87 tamanho amostral obtido para migração impediu chegar a conclusões claras sobre que  
88 comportamentos motivam este processo.

89 Tendo em conta a importância da migração para as dinâmicas dos ecossistemas a nível global, e o  
90 declínio do comportamento migratório devido à ação humana (Kirby et al. 2008), o Capítulo 2  
91 emerge pela necessidade de incentivar a pesquisa sobre as diferenças fenotípicas entre residentes e  
92 migradores, sobretudo no contexto de diferenças comportamentais. Assim, me baseando  
93 essencialmente nos estudos obtidos na revisão sistemática, no capítulo 2 apresento os principais  
94 resultados da literatura sobre migração parcial (fenómeno em que uma espécie é composta por  
95 indivíduos que migram e indivíduos que não migram) e comportamento animal, além de identificar  
96 as principais lacunas do conhecimento sobre o tema. Concluo chamando à atenção da comunidade  
97 científica para a importância do estudo do comportamento migratório nos tempos atuais.

## 98 **CONCLUSÕES**

99 A presente dissertação sintetiza formalmente a literatura sobre o papel do comportamento animal  
100 em processos biogeográficos, e demonstra que diferenças comportamentais podem ajudar a explicar  
101 o sucesso dos indivíduos na expansão do território. A realização de uma revisão sistemática e meta-  
102 análise no capítulo 1 me permitiu mostrar que indivíduos com comportamentos mais ousados e  
103 mais exploratórios podem ser os principais responsáveis pela expansão do território. Através da  
104 avaliação de contexto-dependências, demonstro que indivíduos com menor latência para entrar em

105 novo meio, maior nível de exploração do novo meio e mais rápidos a encontrar um recurso no novo  
106 meio, são os que mais sucesso possuem na expansão do território. Os resultados mostraram ainda  
107 que invasores são geralmente mais exploratórios e mais ativos que nativos, e que dispersores são  
108 mais exploratórios e mais ousados que não dispersores. Assim, o capítulo 1 consegue apresentar  
109 evidências de que diferenças comportamentais em animais podem afetar o sucesso dos indivíduos  
110 na expansão do território. Para além disso, o capítulo 1 se baseia no baixo tamanho amostral obtido  
111 para alguns traços comportamentais e alguns moderadores, para identificar as principais lacunas de  
112 conhecimento no estudo da relação entre comportamento e expansão do território. Por exemplo,  
113 poucos estudos foram coletados que estudaram o processo de migração, apesar deste ser um  
114 processo de extrema importância na dinâmica dos ecossistemas a larga escala. Diante disso, o  
115 capítulo 2 emerge pela necessidade de focalizar a lacuna existente no estudo de como o  
116 comportamento animal pode afetar a propensão para migrar. Deste modo, no capítulo 2 eu  
117 apresento as descobertas mais importantes nesta área de estudo, elaboro possíveis explicações para  
118 as vantagens de cada tipo de comportamento nas estratégias de migração ou residência, e destaco o  
119 papel da ação humana no comportamento migratório. Tudo isto para incentivar a comunidade  
120 científica para a realização de mais estudos sobre o papel das diferenças comportamentais na  
121 migração.

122 Os resultados oriundos desta dissertação mostram que diferenças comportamentais podem  
123 contribuir para o sucesso na expansão do território e ultimamente ajudar a entender que  
124 características tornam as espécies mais aptas a prosperar perante os novos desafios ambientais  
125 impostos pelas mudanças globais.

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## 221 **Capítulo 1**

222

### 223 **The role of behavioral traits in species distribution: a bayesian meta-analysis**

224

225 **ABSTRACT:** Research in animal personality is increasing our understanding of what prevents a  
226 species from colonizing new areas, which is one of the outstanding questions in biogeography.  
227 Some behavioral types can perform better than others in specific stages involved in range  
228 expansion. For example, a high exploratory behavior increases the chances of finding new resources  
229 in novel environments. However, inconsistent results in the literature hindered a definite recognition  
230 of the role of animal personalities on species distributions. I collected data available in the literature  
231 and performed a bayesian meta-analysis to assess which behavioral types are driving range  
232 expansion in the following biogeographical processes: dispersal, migration and invasion. I used  
233 several moderators to try to discern context-dependencies in effect sizes. A hierarchical model, with  
234 effect sizes nested within studies, revealed that more exploratory and bolder behaviors facilitate  
235 range expansion. Also, I found that invasive individuals are more likely to be more exploratory and  
236 more active than natives, while dispersers are generally bolder and more exploratory than non-  
237 dispersers. Yet, the low study sample size obtained for analysis stresses the need to conduct more  
238 primary studies. Results highlight the role of behavioral traits in species distributions and increase  
239 our knowledge about which ecological characteristics might prepare species to endure the current  
240 global environmental challenges.

241

#### 242 **RESUMO**

243 A pesquisa em personalidade animal está aumentando o nosso conhecimento sobre o que previne  
244 uma espécie de colonizar novas áreas, sendo esta uma das principais questões em biogeografia.  
245 Alguns tipos de comportamento podem resultar em melhor desempenho que outros em específicos

246 estágios de expansão do território. Por exemplo, um comportamento mais exploratório facilita a  
247 descoberta de recursos em um novo meio. Contudo, resultados inconsistentes na literatura estão  
248 dificultando um reconhecimento do papel da personalidade animal na distribuição das espécies.  
249 Coletei dados da literatura e realizei uma meta-análise bayesiana para determinar que tipos de  
250 comportamento são responsáveis pela expansão do território através dos processos biogeográficos  
251 de: dispersão, invasão e migração. Fiz ainda uso de vários moderadores na tentativa de identificar  
252 contexto-dependências nos tamanhos de efeito. Em um modelo hierárquico, usando tamanhos de  
253 efeito aninhados dentro dos estudos, mostro que um comportamento mais ousado e mais  
254 exploratório facilita o sucesso na expansão do território. Para além disso, eu demonstro que  
255 invasores são mais exploratórios e mais ativos que nativos, e dispersores são mais exploratórios e  
256 ousados que não-dispersores. Contudo, o baixo tamanho amostral obtido para as análises demonstra  
257 a necessidade de conduzir mais estudos primários. Os resultados realçam o papel dos traços  
258 comportamentais na distribuição das espécies e aumentam o nosso conhecimento sobre que  
259 características ecológicas podem preparar as espécies para resistir aos desafios das mudanças  
260 ambientais.

261

## 262 **INTRODUCTION**

263

264 Differences in behavior among humans are one of the building blocks of our societies, as each  
265 person's personality influences both its own life and the lives of people around. For non-human  
266 animals it might be no different. Individual differences in behavior, formerly considered as noise of  
267 an adaptive mean trait (Réale et al. 2007), are gaining importance as key factors in ecological and  
268 evolutionary processes (Pennisi 2016). Behavioral differences were already shown to have  
269 implications in fitness (Smith & Blumstein 2008), predator-prey dynamics (Sih et al 2003), range  
270 expansion (Duckworth & Badyaev 2007), or even drive communities to collapse (Pruitt &

271 Modlmeier 2015). Moreover, behavioral differences have underlying physiological (Groothuis et al.  
272 2008), genetic (Dochtermann et al. 2015), epigenetic (Verhulst et al. 2016) and heritable (van Oers  
273 et al. 2004) mechanisms. When behavioral differences are consistent both over time and/or across  
274 different contexts, they are termed ‘temperament’ (Réale et al. 2007) or ‘personalities’ (Wolf and  
275 Weissing 2012).

276 A promising topic in the study of animal personalities is their role on species distributions  
277 (Canestrelli et al 2016), where some behavioral types can be the main drivers of range expansion.  
278 Specifically, animal personalities can produce a non-random spatial distribution of behavioral types  
279 if they influence common steps for different biogeographical processes: the decision to abandon a  
280 current area, the ability to move between areas, and the capacity to establish in a new area. The  
281 spatial dynamics of species distributions are primarily shaped by dispersal, migration and invasion  
282 (Cassini 2013). By natural means, species can move between locations through dispersal or  
283 migration, where dispersal is a single, generally solitary one-way movement from one area to  
284 another, and migration is a cyclical, generally collective movement between two areas (Cote et al.  
285 2016). By non-natural means, the invasion process shares similarities with dispersal, but in that case  
286 animals make use of human-mediated transport (e.g. animals accidentally transported with cargo),  
287 which enables them to overcome ecological and geographical barriers (Chapple et al. 2012).  
288 Despite the differences between the processes of dispersal, migration, and invasion, all describe  
289 individual responsiveness to socio-ecological factors and expose individuals to significant costs and  
290 environmental challenges (Bowler and Benton 2005, Blackburn et al. 2011, Chapman et al. 2011a).  
291 Consequently, even within a population, not all individuals successfully move between areas, and  
292 differences in success have been mostly attributed to variation in physiological, behavioral,  
293 cognitive and morphological traits (Clobert et al. 2009). For example, a larger relative brain size,  
294 which is used as a proxy for cognitive ability, has been positively related to invasiveness (Sol et al.  
295 2008) and negatively related to migratory propensity (Sol et al. 2005, Vincze 2016). Several other

296 traits have been shown to influence the propensity of individuals to expand their range, such as  
 297 body size (McCauley et al. 2010, Thorlacius et al. 2015), parental care (Duckworth 2008, Jonker et  
 298 al. 2012) and corticosterone levels (de Fraipoint et al. 2000). However, phenotypic differences  
 299 between individuals that tend to stay and those that tend to depart do not hold in different  
 300 environments, as their nature rely on the suitability of each trait expression to different ecological  
 301 and environmental factors. In this sense, some traits can put weight on the fitness trade-off between  
 302 staying or departing, eventually triggering the decision to depart and ultimately assisting in the  
 303 arrival and establishment in a new area (Bowler and Benton 2005, Chapman et al. 2011a, Chapple  
 304 et al. 2012). Accordingly, studies have shown that individuals with different behavioral types are  
 305 favored in different environments (Riechert and Hall 2000, Sih et al. 2003, Wolf and Weissing  
 306 2012), thus decisions to depart from an area can come from individuals with locally unsuitable  
 307 behavioral types (Table 1).

308 **Table 1** Behavioral traits and predicted effects on range expansion processes. ‘+’ means that a higher behavioral trait  
 309 value (e.g. bolder) relates to higher success in a range expansion stage, and ‘-’ means the opposite. ‘+/-’ means that  
 310 relation is context-dependent or uncertain. The hypothesized relationships are mainly based on Cote et al. 2010,  
 311 Chapman et al. 2011a, Chapple et al. 2012, Canestrelli et al. 2016.  
 312

Behavioral trait	Range expansion processes		
	Dispersal	Migration	Invasion
<b>Boldness</b> (shier → bolder) - reaction towards a risky situation (predators or humans). The bolder individual is more risk-prone (e.g. delay escape response when faced with predator).	+	+	+/-
<b>Exploratory</b> (less exploratory → more exploratory) - reaction towards a new situation (new habitat or new object). The more exploratory individual is more adept to explore new situations.	+	+	+
<b>Aggressiveness</b> (less aggressive → more aggressive) - agonistic interactions towards conspecifics or heterospecifics.	+/-	-	+/-
<b>Activity</b> (less active → more active) - general level of activity in a familiar environment.	+	+/-	+
<b>Sociability</b> (asocial → more social) - tendency to aggregate or to actively search non-aggressive interactions with conspecifics.	-	+	-

313

314 Dispersal tendency is often associated with bolder, asocial, more exploratory, more aggressive  
315 and more active behavioral types (Table 1) (Canestrelli et al. 2016). However, some studies found  
316 that more exploratory, but not bold or asocial individuals, had higher dispersal tendency (Thorlacius  
317 et al. 2015). Others found no differentiation between behavioral types of residents and dispersers  
318 when individuals were experimentally put under predation risk, probably because predator  
319 avoidance dominated dispersal decisions (Cote et al. 2013). Migratory tendency, in turn, has been  
320 linked to bolder behavioral types where bolder individuals might have been compelled to migrate  
321 due to their higher vulnerability to predation in resource scarcity periods (Chapman et al. 2011a,  
322 2011b). Interestingly, human settlements can decrease consumptive predation risk and provide areas  
323 with a year-round supply of resources, which could explain why a study on elk found that bolder  
324 individuals were the ones to remain resident, while shier migrated away from human settlements as  
325 soon as conditions in the mountains became favorable (Found and St. Clair 2016).

326 Invasive species are considered a major biodiversity threat (Vitousek et al. 1996, Simberloff et al.  
327 2013). Although propagule pressure is widely used as a predictor of invasion success, it does not  
328 explain why some species fail to establish in new areas (Sagata and Lester 2009, Chapple et al.  
329 2012). Behavioral research may be able to provide a complementary explanation to invasive  
330 performance (Chapple et al. 2012, Weis and Sol 2016), by suggesting that individuals with  
331 favorable behavioral types can withstand the environmental challenges common to the invasion  
332 process (Chapple et al. 2012). Moreover, behavior plays a crucial role in determining species  
333 interactions and species responses to environmental changes (Wolf and Weissing 2012), so it may  
334 determine what impacts invaders will have once established (Weis and Sol 2016). A study on  
335 bluebirds showed that invaders with more aggressive behavioral types fiercely outcompeted  
336 individuals of native species, therefore increasing their chances to establish in new territories  
337 (Duckworth 2008). However, high aggressiveness can hamper species' capacity to reach high  
338 densities, as aggressive individuals generally acquire larger territories (Duckworth 2008).

339 Therefore, successful invasion might rely on behavioral variation among individuals, where  
340 aggressive individuals pave the way for the latter arrival of more docile individuals (Duckworth  
341 2008). Other study showed that individuals from the front of range expansion were more  
342 exploratory when compared with individuals in long established populations (Martin and Fitzgerald  
343 2005). Individuals inhabiting long established populations may be less exploratory because they  
344 have benefited from available information about locally suitable resources, made possible by the  
345 previous passage of more exploratory individuals.

346 In this study I conduct a meta-analysis to determine which behavioral types are the main drivers  
347 of range expansion. Then I use moderator variables to evaluate context-dependencies affecting the  
348 success of behavioral types along range expansion, and to determine if different behavioral types  
349 are favored in each processes of dispersal, migration or invasion. Many narrative reviews point out  
350 the importance of behavior in biogeography (Cote et al 2010, Chapple et al 2011, Canestrelli et al  
351 2016), but as far as I know, my study is the first to systematically analyse the available literature  
352 and provide general inferences about the role of behavioral differences on species distributions.  
353 Behavior is generally animals' first response to environmental changes (Wong and Candolin 2015).  
354 Thus, in a world with an unprecedented rate of human-induced changes, insights about which  
355 behavioral types motivate range expansion will increase our knowledge of which species will  
356 persist or even thrive in the face of new challenges.

## 357 **METHODS**

### 358 *Literature search*

359 I conducted a literature search for studies published before 17 June 2016 on Web of Science and  
360 Google Scholar databases, with different combinations of keywords commonly found in studies of  
361 animal behavior and range expansion processes (see Appendix A for detailed information). The  
362 search turned up 15,890 studies, which were reduced to 15,513 after duplicate removal. I screened

363 the 15,513 studies by title and abstract using *abstrackr* online platform (Wallace et al. 2012) and  
364 excluded the ones that failed to meet the inclusion criteria (Appendix B for PRISMA diagram). The  
365 full text of all remaining studies was examined closely.

366 In general, animal behavior studies do not follow a well-defined terminology or methodology,  
367 thus I will apply general rules for data extraction. I used animal personality definitions based on  
368 Réale et al. (2007) framework, partitioning personality into five behavioral traits (i) activity; (ii)  
369 aggressiveness, (iii) boldness, (iv) exploratory (v) and sociability (see Table 1 for behavioral trait  
370 definitions). To conduct meta-analysis, I extracted data from studies that systematically measured  
371 any behavior related to one of the five behavioral traits (Table 1), and provided behavioral  
372 comparisons such as those between: i) non-dispersers and dispersers; ii) or residents and migrants;  
373 iii) or native range and introduced range. Both intraspecific and interspecific comparisons were  
374 used, with the latter being restricted to same family comparisons.

#### 375 *Effect size calculation*

376 I computed the Hedge's  $g$  as the standard effect size metric to be used in meta-analysis  
377 (Borenstein et al 2009). The effect size was computed directly from the studies that reported both  
378 the mean behavioral trait value and respective standard deviation for both the group with the least  
379 potential for range expansion (i.e. residents, or non-dispersers or natives) and the group with the  
380 highest potential for range expansion (migrants, dispersers, invaders). Whenever studies did not  
381 provide this information, I proceeded in the following order: (1) tried to collect correlation or linear  
382 regression coefficients assessing a relation between behavioral trait values and the potential for  
383 range expansion (e.g. more exploratory are more likely to disperse farther); (2) collect binary  
384 proportions which normally synthesized behavioral trait variation in two groups (e.g. bold group  
385 and shy group) and assessed what proportion of each group were likely to expand their range; (3)  
386 collect results of statistics based on distributions such as  $t$ -value,  $F$  or  $\chi^2$ ; (4) collect median and

387 interquartile ranges (25% and 75%). To transform the different metrics to Hedge's  $g$ , I used R  
388 software with the `compute.es` package (Del Re, 2013). The only exception was for median and  
389 interquartile ranges, where I followed the procedure in Wan et al (2014) to get approximations for  
390 the mean and standard deviation. Some studies did not report any of the metrics aforementioned or  
391 gave only incomplete data. In that case, I contacted the corresponding author to request the missing  
392 data. Studies that met criteria, but lacked the data needed to compute Hedge's  $g$ , did not report  
393 species-specific data, and experimental studies that explicitly manipulated the physiology or  
394 environmental variables without a control group were not included in the analysis (Appendix A for  
395 PRISMA Diagram).

396 Hedge's  $g$  effect size is centered at 0, where 0 represents no differences between the the two  
397 group means (in my case, no difference between a lower behavioral trait value (less aggressive) and  
398 a higher behavioral value (more aggressive) in their potential for range expansion). A positive  
399 effect size reflects an association between a higher behavioral trait value (e.g. more aggressive)  
400 with a higher potential for range expansion (e.g. more likely to disperse away from home range),  
401 while a negative effect size reflects an association between a lower behavioral trait value (e.g. less  
402 aggressive) and a higher potential for range expansion (e.g. more likely to disperse away from  
403 home range).

#### 404 *Meta-analytical models*

405 To deal with non-independence arising from multiple effects in the same study I built a  
406 hierarchical model and conducted a bayesian meta-analysis for each behavioral trait (Table 2).  
407 Bayesian inference emerges through the combination of prior information with likelihood estimates  
408 to produce a posterior distribution. In my hierarchical model, effect sizes were nested within studies  
409 with random effects for studies to account for some of the within study dependency. Effect sizes  
410 performed on the same individuals, but in different time periods, with different control groups or

411 measuring the same behavioral trait, were lumped as a composite effect size using formulas in  
 412 Borenstein (2009), assuming a correlation coefficient of  $r = 0.5$ . I was unable to account for all  
 413 dependencies (e.g. dependency arising from using the same control group for multiple effect sizes),  
 414 as the low study sample size deterred the possibility of using more complex models.

415 **Table 2** Statistical representation and description of the meta-analytical models.  
 416

<b>Models</b>	<b>Model description</b>
Model without moderator	Each effect size $T_i$ is normally distributed around a true mean $\theta_i$ , with $\theta_i$ being normally distributed around each study mean $\varphi_j$ . These study means are then normally distributed around an overall mean $\mu$ , which represents the summary effect of a behavioral trait on range expansion.
$T_i = N(\theta_i, \sigma_i^2)$ $\theta_i = N(\varphi_{j[i]}, \tau^2)$ $\varphi_j = N(\mu, \omega^2)$	
Model with single moderator	Each effect size $T_i$ is normally distributed around a true mean $\theta_i$ . $\theta_i$ is then normally distributed around a mean determined by study random intercepts $\varphi_j$ and the effect of moderator levels $\beta_k$ ( $k$ represents the number of moderator from 1 to $k$ ) over the random intercept mean $\mu$ . The random intercept mean $\mu$ corresponds to the estimated mean for the effect sizes coded with the moderator level that was set in my model to be the intercept.
$T_i = N(\theta_i, \sigma_i^2)$ $\theta_i = N(\varphi_{j[i]} + \beta_{k[i]} * X_i, \tau^2)$ $\varphi_j = N(\mu, \omega^2)$	

417

418 I assessed the potential for range expansion of each behavioral trait by examining the posterior  
 419 distribution of the summary effect size. The behavioral traits with a 95% credible interval that did  
 420 not overlap 0 were assumed to have an effect on range expansion. Additionally, I tested the  
 421 probability for each behavioral trait to have an effect size value higher than 0 over all Markov  
 422 Chain Monte Carlo (MCMC) iterations, using these probability values to explain the results  
 423 whenever credible intervals were not precise enough to exclude 0. The latter is similar to a one-  
 424 tailed test for a null hypothesis of effect size  $< 0$ , but using Bayesian inference I am actually  
 425 assessing the probability of the effect size being greater than 0 given my data, instead of the  
 426 probability obtaining the effect size estimate, if the null hypothesis (effect size  $< 0$ ) is true.

427 Since my research synthesis addresses different study designs (e.g. experimental and  
 428 observational), different species, and different range expansion processes, I assumed the presence of  
 429 heterogeneity in effect sizes and collected moderator variables to attempt the identification of the  
 430 sources of heterogeneity (Table 3).

431 **Table 3** Moderators and some description of why they were collected for my analysis

Moderators	Justification
How the behavioral trait was measured	Different measurements for the same behavioral traits may not exactly produce the same results (Garamszegi et al 2013)
Experimental or observational study	Animals under observational or experimental conditions can experience a multitude of different factors that potentially constrain their behaviors (Réale et al 2007)
Correlation between behavioral traits in the primary study (I will collect its reported correlation coefficient).	Allows to determine if the potential for range expansion is greater when some behavioral traits are correlated (Sih et al 2012)
Behavioral trait correlation with body mass (I will retrieve their correlation coefficient)	A behavioral type's potential for range expansion may be associated with other traits such as body mass (Chuang and Peterson 2016)
Behavioral measurement level	Behavioral traits can be measured at different taxonomic levels (Réale et al 2007). For example, intraspecific studies may provide different information when compared to interspecific studies (see social organization moderator for an example).
Social organization	Eusocial species, such as the majority of ants, can benefit from a combination of low intraspecific aggression and high interspecific aggression to successfully invade a new location (Holway et al. 1998)
Biogeographical processes	Factors influencing the processes of dispersal, migration and invasion can differ, so I will categorize these processes to discern which behavioral types are most favored in each process (Cote et al. 2010, Chapman et al. 2011a, Chapple et al. 2012)
Taxonomic class	There might be ecological or evolutionary differences between different taxonomic classes such that the behavioral types that most favor range expansion could differ among classes.

432

433 The explanatory power of moderator variables was assessed using bayesian meta-regression  
 434 (Koricheva et al. 2013). For meta-regression, I used a hierarchical model with effect sizes nested  
 435 within studies with random effects for studies and using a single moderator at the effect size level  
 436 (Table 2). I did not conduct any additive or interactive model as the sample size was quite low for  
 437 all behavioral traits (Appendix E Table 1). I am aware that testing each moderator individually  
 438 might give rise to some spurious relations, however choosing only a subset of moderators or not

439 conducting meta-regression at all, could lead to the loss of relevant information. Nonetheless, I  
440 established some rules to conduct meta-regression. I ruled out from meta-regression models, any  
441 behavioral trait with less than ten effect sizes, so I did not performed meta-regression in the  
442 sociability behavior that only had five effect sizes coming from four studies. Moreover, for each  
443 behavioral trait, any moderator level with less than five effect sizes was excluded from analysis. If  
444 the exclusion resulted in only one level with more than five effect sizes, I did not perform meta-  
445 regression for that moderator. This was the case in all behavioral traits for moderators assessing a  
446 correlation between behavioral traits and a correlation between a behavioral trait and body mass  
447 (Appendix E Table 22). I did not perform meta-regression for: activity on the behavioral level  
448 comparison moderator; aggressiveness on the behavioral measurement moderator; boldness on the  
449 type of study and behavioral level comparison moderators; and exploratory on the social  
450 organization, type of study and behavioral level comparison moderators. I did not account for  
451 phylogenetic relatedness in my models, due to time constraints.

452 I used noninformative priors for all model parameters. Normal distributions with very large  
453 variances were used as the priors for means, intercepts and slopes ( $N(0, 10000)$ ), while uniform  
454 distributions were used as priors for variances ( $U(0, 100)$ ). All models ran 3 MCMC chains with  
455 250000 iterations, with the first 25000 iterations being discarded as burn-in. Chain convergence was  
456 checked and achieved in all models.

#### 457 *Publication bias*

458 A major concern in meta-analysis is publication bias, which can arise when systematic reviews  
459 retrieve a non-random sample of studies, or because published literature is biased towards the  
460 publication of significant results (Borenstein et al. 2009). Therefore, to assess the impact of  
461 publication bias while accounting for the non-independent nature of the effect sizes, I performed an  
462 Egger's regression by including the standard error of the effect sizes as the single moderator in my

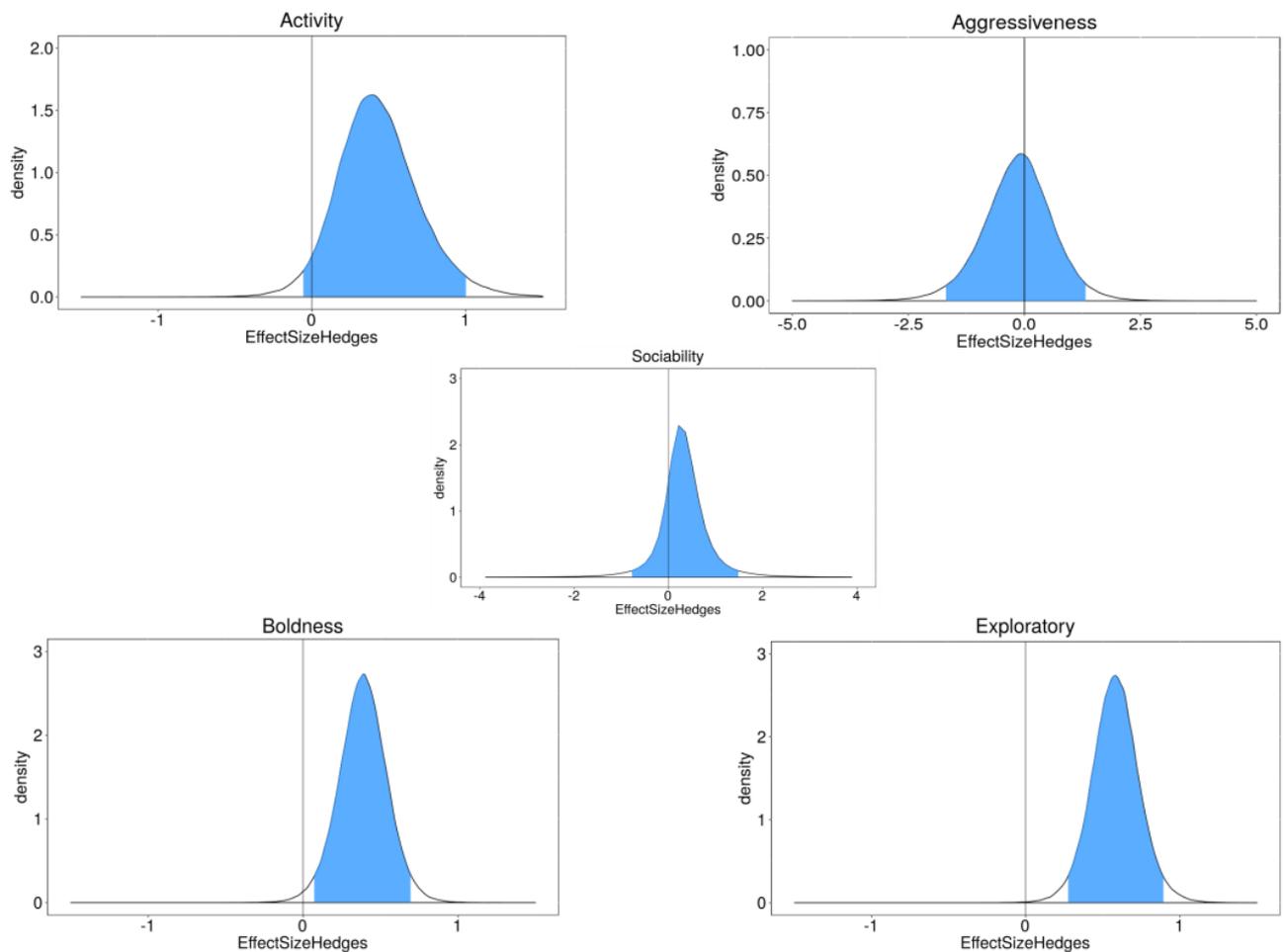
463 hierarchical models. Credible intervals (95%) of the model intercept that do not bracket 0 indicate  
464 publication bias in a given behavioral trait (Sterne and Egger 2005).

## 465 **RESULTS**

466 I selected 903 studies by title and abstract screening. From these, 45 studies passed through the  
467 inclusion criteria and were ultimately used in the meta-analysis. Some studies reported more than  
468 one effect size, as they could have measured multiple behavioral traits and/or multiple species  
469 (Appendix B for PRISMA diagram), totalling 99 effect sizes, distributed among the five behavioral  
470 traits (Appendix D for detailed information). Aggressiveness had the highest number of studies  
471 (18), followed by exploratory and boldness (both 16), activity (14) and lastly sociability (4).

472 In the hierarchical models without moderators, bolder and more exploratory behavioral types had  
473 a higher potential for range expansion, with a summary effect size of 0.3867 (Credible Interval  
474 [0.0720, 0.6967]) (Figure 1) and 0.5822 (CI [0.2745, 0.8975]) (Figure 1), respectively. The summary  
475 effect sizes were also positive for more active (mean = 0.4332) (Figure 1) and more social (mean =  
476 0.3188) (Figure 1) behavioral types, with a more active behavior being highly likely to have a  
477 greater potential for range expansion ( $P(\text{effect size} > 0) = 0.96$ ), but credible intervals for activity  
478 and sociability overlapped zero (Appendix E Table 1). In contrast, the summary effect for  
479 aggressiveness was negative (mean = -0.1290) (Figure 1), but this result only represented a mild  
480 tendency for less aggressive behaviors to have a higher potential for range expansion, because  
481 credible intervals were wide (CI [-1.6940, 1.335]) and probability of having a negative effect size  
482 was only 0.56 (see Appendix E Table 1).

483

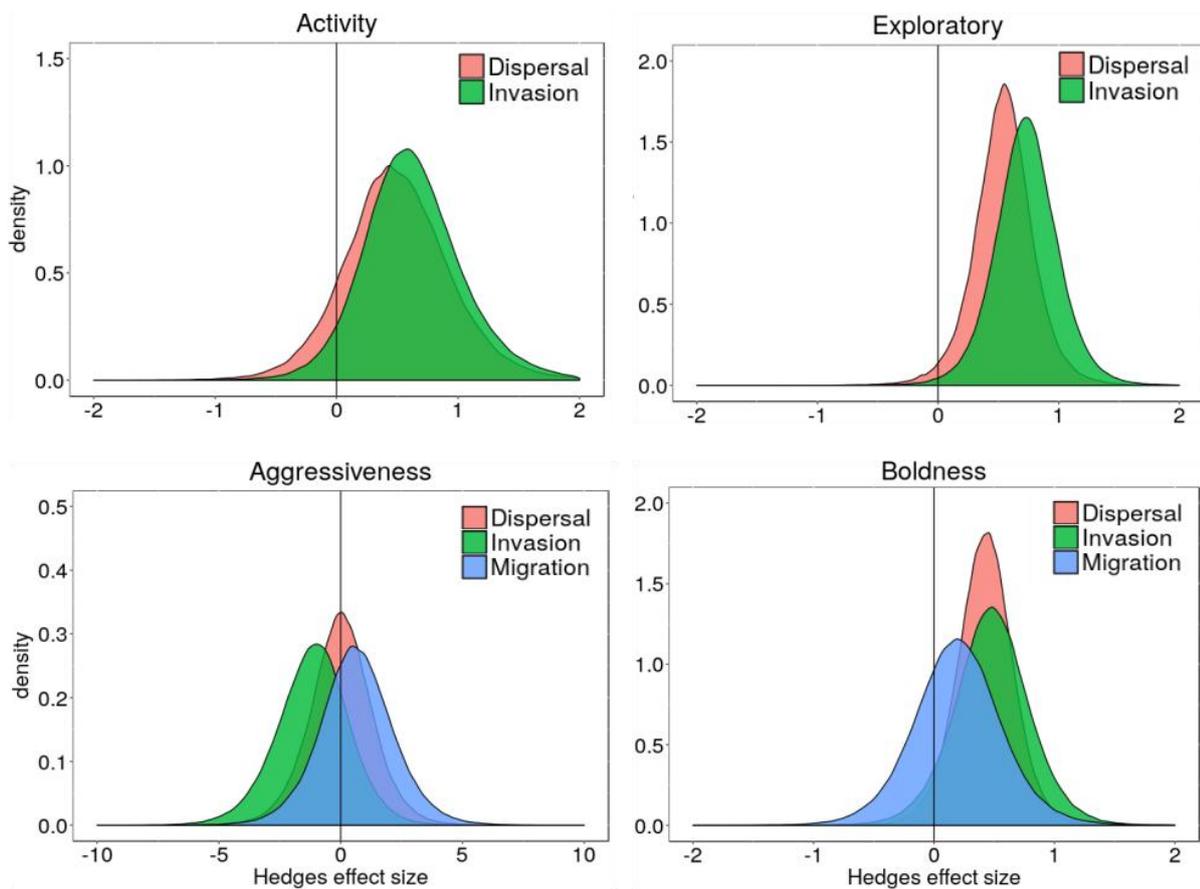


**Figure 1** – Posterior distributions of activity (top left), aggressiveness (top right), boldness (bottom left), exploratory (bottom right) and sociability (middle) behavioural traits obtained for the hierarchical model with effect sizes nested within studies. The area in blue shows the 95% Credible Intervals. A positive effect size means that a higher behavioural trait value (e.g. more active) have a higher potential for range expansion, while a negative effect size means a lower behavioural trait value (less active) have a higher potential for range expansion.

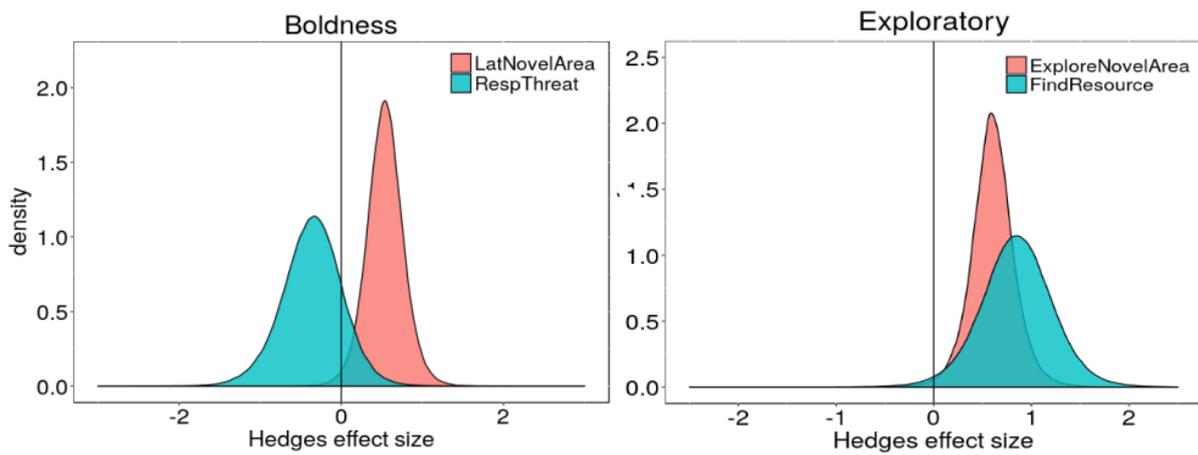
484

485 In the meta-regression models, I found that invasive individuals are more exploratory (mean =  
 486 0.7332, CI [0.1972, 1.2760]) and are also highly likely to be more active ( $P(\text{effect size} > 0) = 0.95$ )  
 487 (Figure 2 and Appendix E Tables 2 - 5). Moreover, dispersers are more exploratory (mean =  
 488 0.5446, CI [0.0253, 1.0560]) (Figure 2) and highly likely to be bolder ( $P(\text{effect size} > 0) = 0.96$ )  
 489 (Figure 2 and Appendix E Tables 2 - 5). Due to the low sample size, I only assessed migration in the  
 490 behavioral traits boldness and aggressiveness, but neither provided evidences of a possible effect on  
 491 migration (Figure 2 and Appendix E Tables 3, 4).

492 Exploratory individuals who led range expansion scored higher on measurements of activity in a  
493 novel area (mean = 0.6050, CI [0.1577, 1.0640]), and were faster in finding a resource in a novel  
494 area (mean = 0.8490, CI [0.0951, 1.5860]) (Figure 3). Additionally, in boldness tests, individuals  
495 who led range expansion had a shorter latency to enter a novel area (mean = 0.5401, CI [0.0859,  
496 1.0020]) (Figure 3).



**Figure 2** – Posterior distributions of activity (top left), exploratory (top right), aggressiveness (bottom left), and boldness (bottom right) for models assessing the moderator ‘biogeographical process’. Distributions refer to the levels of dispersal (in salmon color), invasion (green) and migration (blue). Activity and exploratory behaviors had each less than 5 effect sizes on migration, so migration was excluded from activity and exploratory behaviors models.



**Figure 2** – Posterior distributions for boldness (left) and exploratory (right) behaviors for models assessing moderator ‘behavioral measurement’. For boldness behavior the measurements of latency to enter a novel area (LatNovelArea, in salmon color) and response to threat (RespThreat, in turquoise color) were used as moderator levels. For exploratory behavior the measurements of exploration rate of a novel area (ExploreNovelArea, in salmon color) and response to threat (RespThreat, in turquoise color) were used as moderator levels.

497 Regarding the social organization of the studied species, my models showed that bolder  
 498 individuals from solitary species have higher potential for range expansion (mean = 0.7638, CI  
 499 0.0595, 1.4750]) (Appendix E Table 16). Furthermore, individuals pertaining to the classes  
 500 Actinopterygii and Aves had a higher success in range expansion if they expressed a more  
 501 exploratory behavior (mean = 0.6677, CI [0.1503, 1.1780] for Actinopterygii; and mean = 0.5347,  
 502 CI [0.0292, 1.1290] for Aves), although those were the only levels with enough sample size to be  
 503 included in the model (Appendix E Tables 6 – 9).

504 Model results failed to show evidence that the type of study design (only aggressiveness and  
 505 activity were assessed) (Appendix E Tables 18 – 19) or the behavioral measurement level (only  
 506 aggressiveness was assessed) (Appendix E Table 21) moderators influenced the outcome of the  
 507 relation between a behavioral type and range expansion.

508 Finally, Egger’s regression led me to conclude that publication bias was absent in all behavioral  
 509 trait hierarchical models (Appendix F, Table 1).

510 **DISCUSSION**

511 Range expansion works as a main architect of species distributions. However, not all individuals  
512 are actors in species range expansion, and phenotypic differences are deemed crucial in explaining  
513 why some individuals decide to stay while others decide to leave (Chuang and Peterson 2016). By  
514 statistically summarizing literature findings, I show that bolder and more exploratory behavioral  
515 types are the main behavioral drivers of species range expansion. Specifically, range expansion was  
516 related to individuals with a shorter latency to enter a novel area (bolder), a higher exploration rate  
517 and that were faster at locating a resource in a novel area (more exploratory). I also show that  
518 invaders are more active and more exploratory than natives, and dispersers are more exploratory  
519 and bolder than non-dispersers. These results provide a formal evidence that behavioral effects on  
520 range expansion are meaningful and widespread in nature.

521 For an individual maladapted to his current environment, the decision to depart in search of better  
522 conditions is easily the best strategy. However, this decision introduces new environments and  
523 considerable challenges, which could lead to fitness costs and ultimately survival (Bowler and  
524 Benton 2005, Bonte et al. 2012). To withstand these adversities, individuals should carry  
525 morphological, physiological and/or behavioral characteristics adapted for unpredictable  
526 environments (Clobert et al. 2009). Here I reveal, for the exploratory trait, that being more active in  
527 a novel area and quicker to find resources are the strongest predictors of success in range expansion.  
528 Higher exploration rates can speed up the spatial recognition of new surroundings, while increasing  
529 the possibilities of finding new and suitable resources. In fact, measuring exploratory behavior as  
530 exploration rate, or as time to find a resource, might be interchangeable, as a greater exploration  
531 rate expands the search area, which eventually increases the probability of finding a suitable  
532 resource. In my synthesis, this notion was supported by the only study who assessed both types of  
533 measurements, where individuals of the invasive delicate skink (*Lampropholis delicata*) were more  
534 active in novel environments and also faster at locating a basking site than individuals from the  
535 native garden skink (*L. guichenoti*) (Chapple et al. 2011).

536 The decision to leave the current environment and enter in an uncertain one sets the first stage of  
537 range expansion. Here I show that individuals with a shorter latency to enter a novel area have a  
538 higher potential for range expansion. By being the first to depart from unfavorable environments, an  
539 individual might anticipate greater dangers, thus reducing the costs of staying in a harmful place  
540 (Bowler and Benton 2005). Yet, benefits of departure have to counterbalance with potential costs  
541 enough, so that transient individuals could potentially survive, and ultimately establish and prosper  
542 in a new location. Thus, the success in range expansion might depend on an interplay between  
543 being bold enough to leave the current location and being more exploratory in new environments.  
544 Actually, four out of the five studies in my synthesis that assessed both behavioral traits, found that  
545 individuals with higher potential for range expansion were bolder and more exploratory (Marentette  
546 et al. 2011, Mettke-Hofmann et al. 2013, Brodin et al. 2013, Debeffe et al. 2013). The only study  
547 with opposing results was a study on migration, where residents lived in close proximity to human  
548 settlements (Found and St. Clair 2016). I argue that human activity disrupted the conditions  
549 normally found in natural environments.

550 In natural environments, higher boldness translates into an increased chance of being predated  
551 (Sih et al. 2003). Human activity can reverse the consequences of a bolder behavior, as bolder  
552 individuals are known to better withstand human proximity (Carrete and Tella 2011, Vincze et al.  
553 2016). This consequently allows them to live close to human areas, which are characterized by  
554 diminished predation risk (Beale and Monaghan 2004, Møller 2012) and year-round provision of  
555 resources (Newsome et al. 2015). I emphasize that human activity has been related to declines in  
556 migratory behavior (Chapman et al. 2011a, Hebblewhite and Merrill 2011), and despite numerous  
557 findings showing that a bolder behavior predicts urban adaptation (Møller 2008, Sol et al. 2013,  
558 Samia et al. 2015), it is surprising that only one study assessed the linkage between migration,  
559 behavioral traits and human activity (Found and St. Clair 2016). In fact, migration was the least  
560 studied biogeographical process in my synthesis by a large margin, even though it plays a crucial

561 role on ecosystem dynamics across vast geographical areas (Dingle and Drake 2007). When we  
562 look at partial migration, where only a portion of a population migrates while others remain resident  
563 (Chapman et al. 2011a), we could think that behavioral differences have the potential to provide  
564 meaningful insights to migratory tendency. Some studies already marked the importance of  
565 behavioral types in migration propensity (Mettke-Hofmann et al. 2009, Nilsson et al. 2010,  
566 Chapman et al. 2011b), but the lack of studies in my synthesis hindered the possibility to reach  
567 valuable generalizations and should highlight the need to conduct further research.

568 Dispersal is undoubtedly a harsh decision to dispersers and despite factors exist that could  
569 disclose benefits for dispersal (e.g inbreeding avoidance), animals are now confronted with the  
570 spread of human intervention (Ceballos et al. 2015). In the face of these contemporary challenges,  
571 many individuals are left with the choice to disperse or perish. However, not all individuals have the  
572 same motivation to depart nor the same capacity to survive (Bowler and Benton 2005), and I show  
573 that dispersers are generally bolder and more exploratory than non-dispersers. As aforementioned,  
574 bolder and more exploratory behaviors could indeed increase the success of individuals along range  
575 expansion. Nonetheless, a bolder and more exploratory behavior during transience could make  
576 individuals more prone to predation (Cote et al. 2010a), as they can be respectively less vigilant and  
577 more active. Hence, the secret for survival perhaps lies on the ability to flexibly adjust the behavior  
578 in response to current conditions, or in that selective filters might act to reduce the mean levels of  
579 exploratory and boldness behaviors to an acceptable intensity (Weis and Sol 2016).

580 Differently from dispersal, invasion depends on human activity, and is widely accepted as one of  
581 the major contemporary threats to biodiversity (Vitousek et al. 1996, Simberloff et al. 2013). Thus,  
582 knowing what predicts invasion success is of tremendous importance to assist management  
583 decisions. Behavioral differences have been recently put forth as important predictors of invaders  
584 success and invaders' impact on ecosystems (Weis and Sol 2016). I found that invasive individuals

585 are generally more exploratory and more active than their native counterparts. To become an  
586 invader, an individual must be transported by a human vector to a new location (Blackburn et al.  
587 2011). Once in the new location, individuals need to exit the transport vector and search the new  
588 environment for food and shelter (Chapple et al. 2012). A more exploratory behavior can be crucial  
589 at this stage, allowing a quicker retrieval of the information needed for survival (if any exists).  
590 However, when an individual arrives at a new place, there is a high probability that some other  
591 species has arrived before and is already exploiting the same resource. In this case, being more  
592 active once established can allow the individuals to increment resource exploitation, consequently  
593 reinforcing population growth. Other possibilities for high activity are that invaders can be released  
594 from predators and/or competition in their invaded environment (Colautti et al. 2004), being thus  
595 allowed to move more freely and consequently the higher levels of activity might be the result of  
596 the conditions in the invaded area and not an individuals' intrinsic advantage to withstand invasion.

597 There are many published studies linking aggressiveness with range expansion (Holway and  
598 Suarez 1999, Hudina et al. 2014). However, I was unable to discern a clear pattern of its effect on  
599 range expansion success. Aggression might act on range expansion in complex ways that were not  
600 possible to be accounted for with my modest sample size. For example, eusocial species, such as  
601 ants, might benefit from low intraspecific aggression to form cooperative supercolonies, and  
602 simultaneously from high interspecific aggression to outcompete other species for resources  
603 (Holway et al. 1998, Dejean et al. 2010). I gathered as moderators both the social organization of a  
604 species and the level of behavioral trait comparison, but the low sample size deterred me from  
605 testing interactions between moderators.

606 Despite the existence of some theoretical and empirical studies showing a relation between  
607 sociability and range expansion (Cote and Clobert 2007, Fogarty et al. 2011), I could not reach any  
608 conclusion on sociability, as it was the least studied behavioral trait, with less than half the number

609 of studies on activity (the second last). More than ten years ago a well set-up experimental study  
610 with lizards clearly showed that high population density motivates the dispersal of asocial  
611 individuals, whereas low population density leads to the dispersal of social individuals (Cote and  
612 Clobert 2007). Asocial individuals probably dispersed when in high densities because they prefer to  
613 minimize social interactions, while the opposite explained the dispersal of social individuals (Cote  
614 and Clobert 2007). This iconic study showed that dispersal could be triggered by behavioral types  
615 experiencing unfavorable ecological conditions. Thus, it is surprising that a decade after this study I  
616 could only retrieved a handful of studies linking sociability and range expansion.

617 Although I tested each behavioral trait at a time, a single behavioral type will never be the sole  
618 explanation for range expansion in a given context. Most of the times, individuals rely on a set of  
619 traits that promote their ability to expand species range (Dingle 2006, Duckworth 2008, Sih et al.  
620 2012, Chuang and Peterson 2016). I collected the correlation coefficients reported in primary  
621 studies, assessing relations among behavioral traits and between a behavioral trait and body mass.  
622 This strategy would have allowed me to see if some relation between traits was important in  
623 predicting the success in range expansion, but my purposes did not come to fruition as very few  
624 studies assessed these relations. Range expansion dynamics could encompass several trait  
625 correlations, so I underline that in the future we should have more primary studies reporting  
626 correlations of behavioral traits against other behavioral and non-behavioral traits.

627 Anthropogenic stressors are changing species distributions, leading to dramatic range shifts  
628 among many taxa (Wong and Candolin 2015). Thus, we should integrate the knowledge acquired  
629 from multiple fields to obtain a more complete image of what makes species succeed in new  
630 environments. Coming from a relatively new research area in ecology, the results from this study  
631 have the power to pave the way for an acknowledgement of the role of behavioral traits on species  
632 distributions. Nonetheless, my extensive literature review still stresses the need to conduct more

633 primary studies, as many results were probably undermined or cryptic due to the low sample size.  
634 Nonetheless, the prospects are good, as the recent excitement of the scientific community led to a  
635 tremendous increase in the number of studies assessing the behavioral effects on ecological and  
636 evolutionary processes (Pennisi 2016). I would not be surprised if in a couple of years stronger  
637 evidences could be gathered to validate the notion that behavior may in fact matter to species  
638 distributions.

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815 **Capítulo 2**

816

817 **Do residents behave differently than migrants? Describing how behavioral**  
818 **variation can contribute to partial migration**

819

820 **ABSTRACT**

821 Migration is critical for ecosystem dynamics across space and time, yet it is perhaps the least  
822 understood form of animal movement. An interesting question is why, within a same species, some  
823 individuals migrate while others remain resident in a phenomenon called partial migration.  
824 Behavioral differences might be one of the answers for this question, where the expression of  
825 different behavioral types makes individuals more or less fit for either the migratory or resident  
826 strategy. By building arguments upon results from a systematic review, I investigate how and why  
827 residents and migrants differ in their behavior. Additionally, I attempt to identify the main  
828 knowledge gaps, and suggest research topics. I argue that the rise in human activity is shifting the  
829 behavioral differences between residents and migrants usually observed in natural settings. Being  
830 true, it is a concerning matter and one that definitely merits further research. Migratory behavior is  
831 declining due to the threats posed by global changes, so scientists should act promptly to understand  
832 what conditions must be kept for the survival of migrant species and all species that depend on  
833 them.

834 **RESUMO**

835 A migração é crucial para as dinâmicas dos ecossistemas ao longo do espaço e do tempo.  
836 Contudo a migração é possivelmente a forma de movimento animal menos compreendida. Uma  
837 questão interessante é porque, numa mesma espécie, alguns indivíduos migram enquanto outros  
838 permanecem residentes, num fenómeno conhecido como migração parcial. As diferenças  
839 comportamentais podem ser uma das respostas para esta questão, onde a expressão de diferentes  
840 tipos de comportamento torna os indivíduos mais ou menos aptos para a estratégia de migração ou a  
841 estratégia de residência. Me baseando em resultados duma revisão sistemática para a construção de  
842 argumentos, eu revelo algumas descobertas interessantes sobre o como e o porquê de residentes e  
843 migrantes possuírem diferentes tipos de comportamento. Para além disso, eu procuro identificar as  
844 principais lacunas de conhecimento na tentativa de incentivar mais pesquisa neste campo. Por fim,  
845 eu argumento que a crescente atividade humana está alterando as diferenças comportamentais,  
846 geralmente encontradas em meios naturais, entre residentes e migrantes. Se isso for verdade, é um  
847 assunto preocupante que urge mais investigação. O comportamento migratório está em declínio  
848 devido às ameaças das mudanças globais, por isso os cientistas devem agir prontamente para  
849 entender que condições têm de ser mantidas para salvar os migrantes e todas as espécies que  
850 dependem deles para sobreviver.

## 851 **INTRODUCTION**

852 Animal migration is arguably the most impressive, but least understood, form of animal  
853 movement. Each year billions of animals from all branches of the animal kingdom, embark on  
854 seasonal journeys in search for food, mates, to avoid predators or to escape from severe  
855 environmental conditions (Chapman et al. 2012). For some animals, these journeys cover vast  
856 geographical areas shaping species distributions across space and time. By periodically moving  
857 between environments migrants become important pieces in ecosystem structure and dynamics, and  
858 their travels are critical for nutrient transport and trophic interactions (Brodersen et al. 2008,

859 Chapman et al. 2012). Yet, migratory species are facing increasing challenges with global changes  
860 in climate, phenology, invasive species, exploitation and land-use changes (Kirby et al. 2008).  
861 These challenges are modifying or even interrupting the migratory behavior of many animals  
862 (Chapman et al. 2011a, Møller et al. 2013), which can lead to detrimental effects on ecosystem  
863 dynamics (Brodersen et al. 2008) and species persistence (Chapman et al. 2011a). For example,  
864 some predators rely on seasonal abundance of migratory prey to gain the needed energy to  
865 withstand periods of prey scarcity. Without migratory prey, some of these predators would not  
866 survive. Despite the importance of migration for ecological and evolutionary processes at all levels,  
867 migration is perhaps the least understood process of animal movement.

868 An intriguing migratory phenomenon is partial migration, where in a given species or population,  
869 some individuals decide to migrate while others remain resident. Partial migration is widespread in  
870 nature, and it is believed that almost all migratory species are composed of a mixture of resident  
871 and migratory individuals (Chapman et al. 2011a). Understanding what causes individuals to differ  
872 in migratory tendency is critical to getting the bigger picture of what drives migration. Partial  
873 migration studies can provide clearer results about the proximate and ultimate causes of migration,  
874 because they usually compare species or individuals that closely resemble each other, except for the  
875 difference expressed in migratory tendency. For instance, migrants have been shown to have a  
876 smaller body size than residents (Skov et al. 2011). Smaller-sized individuals could migrate to avoid  
877 predation or because they might be competitively inferior and thus unable to acquire the needed  
878 resources during scarcity periods (Chapman et al. 2012). Also, studies found that migrants have a  
879 smaller relative brain size and are less innovative than residents (Sol et al. 2005, Vincze 2016). One  
880 hypothesis is that migrants are able to use public information by observing residents' behaviors and  
881 do not need to develop their own strategies through trial-and-error (Mettke-Hofmann et al. 2013).  
882 Also, residents withstand stronger environmental fluctuations in their environment and a better  
883 cognitive capacity might be needed to adjust their behavior and adapt promptly (Sol et al. 2005).

884 The aforementioned phenotypic differences between residents and migrants are probably governed  
885 by a set of trade-offs, where migration is the more energetically demanding strategy possibly  
886 hindering body and brain size enlargement.

887 There is a growing interest in investigating behavioral differences between residents and migrants  
888 (Chapman et al. 2011b). Different behaviors are known to be favored in different environments  
889 (Riechert and Hall 2000, Wolf and Weissing 2012) and the expression of a given behavioral type  
890 could lead to an increased suitability for either the resident or the migratory strategy. Here, we  
891 define behavioral type as the behavior expressed by an individual in each of the five behavioral  
892 traits axes: activity, aggressiveness, boldness, exploratory and sociability (Réale et al 2007). For  
893 example, an individual with a more active behavioral type is scored higher in the activity axis.

894 Partial migration studies might gain explanatory power through the inclusion of individual  
895 variation in behavioral traits, yet, to date, very few studies assessed behavioral differences between  
896 residents and migrants (Chapman et al. 2011a). The lack of studies could be attributed to the recent  
897 nature of behavioural trait research within ecology, along with logistical difficulties to collect both  
898 behavioral and migratory data (Nilsson et al. 2014). The present work resulted from a systematic  
899 review on the role of behavioral traits in species distributions (see Chapter One), which realized a  
900 deficit in the amount of studies assessing migration in comparison to dispersal or invasion. I intend  
901 to summarize the main findings of the studies gathered in my systematic review and encourage  
902 further research on the exciting link between behavioral differences and migration.

## 903 **SYSTEMATIC REVIEW OF STUDIES AND OBSERVED PATTERNS**

### 904 *Literature search and database*

905 I searched the Web of Science and Google Scholar databases for studies published before 17 June  
906 2016 using a mixture of terms used for behavioral traits and biogeographical processes (Appendix A

907 for detailed information). The search returned 15,890 studies, turned into 15,513 after duplicate  
908 removal. These studies were reviewed by title and abstract using *abstrackr* online software (Wallace  
909 et al. 2012) and excluded if they failed to meet my criteria (Appendix B for PRISMA diagram).  
910 Studies that met criteria went through full text revision and given further examination if they  
911 explicitly measured behavioral traits (activity, aggressiveness, boldness, exploratory and  
912 sociability), and provided behavioral comparisons between residents and migrants. I defined  
913 behavioral traits primarily according to Réale et al. (2007) framework. I considered five behavioral  
914 traits: (i) *activity*, which is the general level of activity in a familiar environment; (ii)  
915 *aggressiveness*, defined by the display of agonistic interactions towards conspecifics or  
916 heterospecifics; (iii) *boldness*, as the reaction towards a risky situation (e.g. predators or humans);  
917 (iv) *exploratory*, which is the reaction towards a new situation (e.g. novel object) or the level of  
918 activity in a novel environment; and lastly (v) *sociability* defined as the tendency to aggregate or to  
919 actively search non-aggressive interactions with conspecifics.

920 I calculated the Hedge's *g* effect size to gather a standardised and comparable measure of the  
921 effect of behavioral types in migratory propensity. The effect size was computed from studies that  
922 reported the mean behavioral trait value and respective standard deviation for both the residents and  
923 the migrants. If studies did not report this data I tried the following in order: (1) collect binary  
924 proportions in studies that split behavioral trait variation in two groups (e.g. bold group and shy  
925 group) and assessed what proportion of each group were likely to be either migrant or resident; (2)  
926 collect results of statistics based on distributions such as t-value, F or  $\chi^2$ ; (3) collect median and  
927 interquartile ranges (25% and 75%) of the behavioral measures in both migrants and residents. To  
928 transform the different metrics to Hedge's *g* I used R software with the *compute.es* package (Del  
929 Re, 2013), unless the data collected were the medians and interquartile ranges, where I followed the  
930 procedure in Wan et al (2014) to get approximations for the mean and standard deviation. If studies

931 provided relevant information, but did not report all the needed data to calculate the effect size, I  
932 contacted the authors requesting the missing data.

933 In my study, a positive effect size reflects an association between a higher behavioral trait value  
934 (e.g. more aggressive) and a higher migratory propensity, while a negative effect size will reflect an  
935 association between a lower behavioral trait value (e.g. less aggressive) and higher migratory  
936 propensity. Due to low study sample size, I did not compute a summary effect and therefore I only  
937 assessed effects individually.

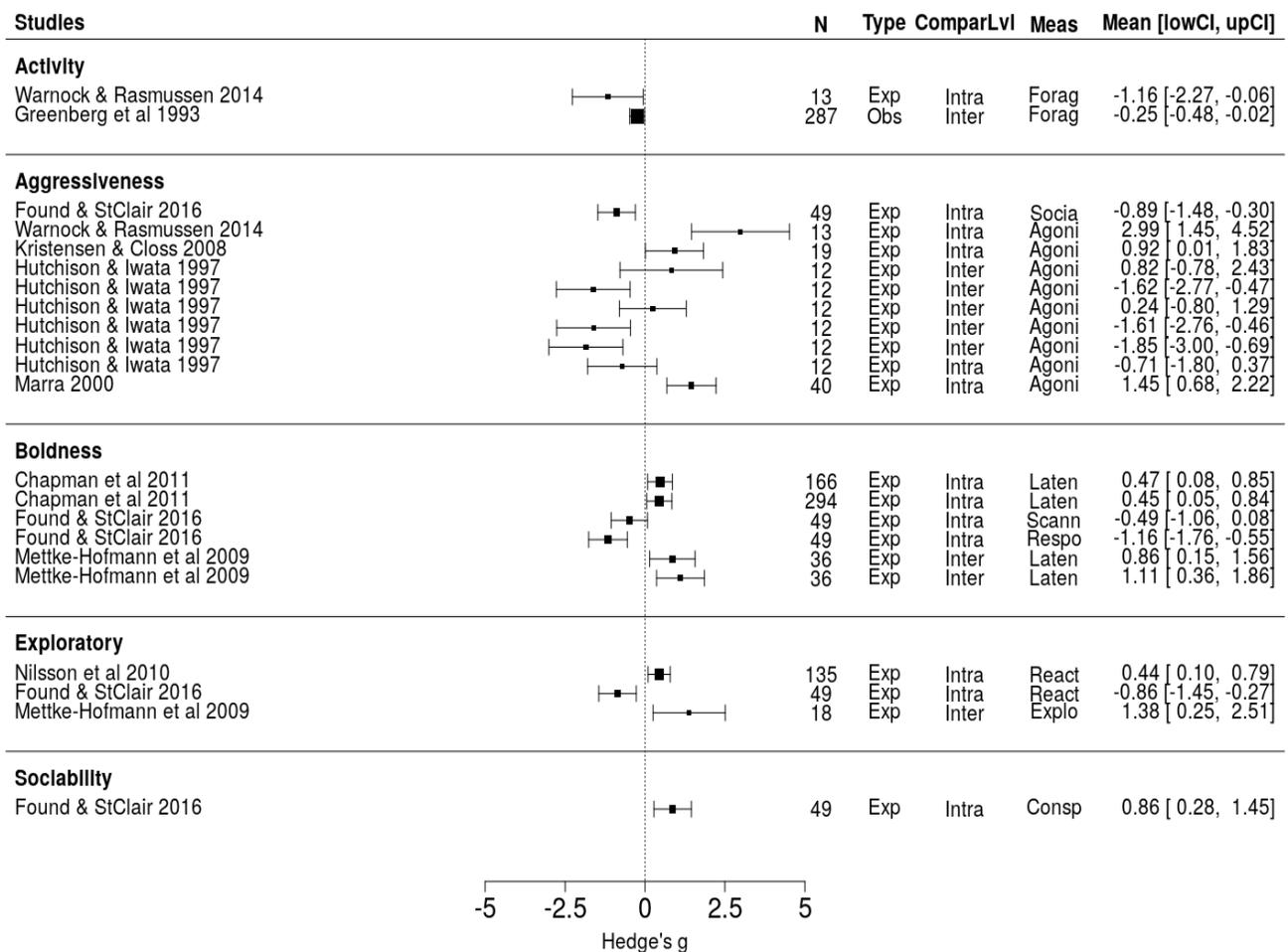
938 To explore some research and data patterns I collected variables describing: how a behavioral  
939 trait was measured; if the study was experimental or observational; if there was a correlation  
940 between different behavioral traits assessed in the primary study; if there was a correlation between  
941 the behavioral trait and body mass; species taxonomic class; behavioral comparison level (i.e. if  
942 study compared the behavior of individuals within a species, of between different species). These  
943 variables can allow a descriptive analysis about observable patterns in the data and the investigation  
944 of research biases.

#### 945 ***Brief quantitative description of studies***

946 A total of 9 studies were collected for all behavioral traits, providing information for 12 migratory  
947 species belonging to three taxonomic classes (Mammalia, Aves and Actinopterygii). Four studies  
948 were conducted in the present decade, three in the 2000s and two in the 1990s. Some studies  
949 contributed with more than one effect size to my data set as they performed analysis on multiple  
950 traits and/or multiple species. For example, a study investigating behavior and migratory tendency  
951 in two species will have two effect sizes in my data set, representing the results obtained for each  
952 species. Therefore, I collected a total of 22 effect sizes (more details in Figure 1). Aggressiveness  
953 had the highest number of effect sizes (10) coming from 5 studies and sociability was the least  
954 studied behavioral trait with only one effect size (Figure 1).

955 *Are migrants really less active?*

956 High levels of activity can increase foraging opportunities and promote an updated knowledge of  
 957 the environment. However, high activity can also increase susceptibility to predation, by means of  
 958 increased spatial and time exposure to predators (Sih et al. 2012). In an environment where  
 959 predation risk is not excessively augmented due to an individual's activity, we might hypothesize  
 960 that more active individuals will outcompete less active ones. In fact, resident bull trout individuals  
 961 showed higher foraging activity than migratory individuals and were better at competing for  
 962 resources against the sympatric brook trout (Warnock and Rasmussen 2014). Also, in a comparison



**Figure 1** – Forest plot with behavioral trait grouping for effect sizes collected in migration systematic review. N column shows sample size. Type column shows study type, where Exp – Experimental and Obs – Observational. ComparLvl column corresponds to whether behavior was compared within individuals of the same species (Intra – Intraspecific) or between different species (Inter – Interspecific). Meas column corresponds to type of behavioral measurement where Forag – Foraging rate, Socia – Social rank, Agoni – Agonistic interactions, Laten – Latency to enter novel area, Scann – Scanning, Respo – Response to threat, React – Reaction to novel object or food, Explo – Exploration rate in novel area, Consp – Conspecific approximation

963 of two closely related birds, resident Vireos had a higher foraging rate than migratory Vireos  
964 (Greenberg et al. 1993). These results show that less active individuals might not be able to acquire  
965 the needed resources to survive being forced to migrate in search for places with higher resource  
966 availability. Additionally, when arriving at new places, migrants can face territorial residents with  
967 established territories, and low activity levels can be useful to decrease the number of agonistic  
968 interactions with residents. In contradiction, migratory individuals of the yellow American eel have  
969 been shown to have higher activity levels than residents (Castonguay et al. 1990), however  
970 migratory individuals were caught while migrating, which could explain their high activity levels.

971 I argue that activity, measured as the level of activity in a familiar environment (Réale et al.  
972 2007), is a controversial measurement in migrants who periodically change between different  
973 locations. It is possible that when migrants reach the end of a migratory journey, the level of activity  
974 in the arrival area reflects exploratory behavior instead of activity behavior. When some time passes  
975 since arrival, exploration should be considered stabilized and only then, levels of activity should  
976 reflect the ones expected for the activity trait. Knowing which moment marks the end of exploration  
977 is undoubtedly challenging, thus I can only recommend that activity studies on migrants should not  
978 be performed just after migrant arrival.

#### 979 ***Do residents aggressively expel migrants?***

980 As activity, aggressiveness could also lead to competition superiority. The display of agonistic  
981 behavior is critical in the establishment and maintenance of dominance hierarchies (Brien et al.  
982 2013) which can translate in higher food acquisition (Adams et al. 1995). In environments with  
983 seasonal abundance of resources, higher levels of aggression can guarantee access to the resources  
984 needed for survival while mitigating the risks of staying resident (Chapman et al. 2011a). In these  
985 environments, less aggressive individuals might be unable to acquire resources in scarcity periods,  
986 being left with the decision to migrate or starve. Additionally, more aggressive individuals are

987 known for their lack of social interactions (Found and St. Clair 2016), which could explain why  
988 they avoid a collective movement such as migration, whenever possible. Following these  
989 interpretations, we could expect a negative relation between aggressiveness and migration  
990 propensity, but results in the literature are far from conclusive. In comparisons between and within  
991 salmonid species, migrant individuals showed lower aggressive levels than residents (Hutchison  
992 and Iwata 1997). A study on elk reached similar results with resident individuals displaying more  
993 agonistic behavior than migrants (Found and St. Clair 2016). In contrast, two studies on trout  
994 showed that migratory individuals were more aggressive than residents (Kristensen and Closs 2008,  
995 Warnock and Rasmussen 2014). Resident individuals are generally considered more aggressive, but  
996 the establishment of social hierarchies can lead to the decrease of aggression once the positions are  
997 established (Bachman 1984). High levels of aggression can also increment costs in terms of energy  
998 expenditure (Harwood et al. 2002), hence when resources are scarce, residents might decrease their  
999 agonistic behavior, whereas migrants travelling in large densities to resource plentiful areas can  
1000 increase their agonistic behavior to attain a competitive advantage in the new environments.

#### 1001 ***Bold enough to leave or bold enough to stay?***

1002 Partial migration has been attributed to individual differences in predation risk, where migrants  
1003 typically leave to escape predation (Chapman et al. 2011a). For example, a study on common  
1004 bream, showed that migrants had higher vulnerability to predation due to their smaller body size  
1005 (Skov et al. 2011). In the context of behavioral traits, boldness is tightly related to predation risk,  
1006 with bolder individuals being less wary of predation risk and thus more likely to get predated (Sih  
1007 et al. 2012). Whenever predation risk is high, bolder individuals could suffer high mortality, unless  
1008 they switch to a more cautious behavior or depart from the current area (Sih et al 2012).  
1009 Nonetheless, bolder individuals should thrive in environments with low predation risk, as shier  
1010 individuals might be overly cautious and miss out good opportunities to perform fitness enhancing

1011 activities (Sih et al. 2003). An explanation to partial migration might lie on a trade-off between  
1012 predation risk and resource availability, such that when food resources are abundant it might be  
1013 worth for bolder individuals to stay, but when resources become scarce, residency can become too  
1014 costly and ultimately motivate their decision to migrate (Chapman et al. 2012).

1015 Using latency to enter a novel room as a measure of boldness, studies on fish and birds have  
1016 shown that migratory individuals entered the novel room more promptly, being more risk-prone and  
1017 probably more susceptible to predation (bird: Mettke-Hofmann et al. 2009, fish: Chapman et al.  
1018 2012). On the other hand, increasing human presence around the globe can lead to high levels of  
1019 perceived risk by shy individuals, turning the tables in favor of bold residency and shy migration  
1020 (e.g. Found and St. Clair 2016), specially if humans do not predate or exert low predation pressure  
1021 upon the migratory species. In fact, bird urbanization is sometimes associated with migratory  
1022 individuals that progressively lost their migratory propensity, because of the year-round supply of  
1023 resources and the milder temperatures in urban areas (Møller et al. 2013). By being able to better  
1024 withstand human presence as evidenced by lower flight initiation distance and lower vigilance rates,  
1025 bolder elk remain resident in peri-urban areas while shy elk migrated away from human  
1026 settlements. Migrant elk only returned seasonally when the severe weather in the mountains forced  
1027 them descend to lower elevation and back to the proximity of human settlements (Found and St.  
1028 Clair 2016).

### 1029 ***Can exploration explain partial migration?***

1030 An innate curiosity makes more exploratory individuals adept of finding novel resources either in  
1031 new environments or familiar ones (Sih et al. 2012). Two ways to measure exploratory behavior are  
1032 the level of activity in a novel environment and the latency to approach a novel object or food in  
1033 either a new or familiar environment (Réale et al. 2007). Intuitively, migrants should be selected for  
1034 more exploratory behaviors because it gives them the ability to rapidly assess high and low-quality

1035 areas and thrive in their newly arrived environments. A comparison of two closely related bird  
1036 species revealed that migrants were faster explorers of a novel cage than residents (Mettke-  
1037 Hofmann et al. 2009). A study on the same species as Mettke-Hofmann et al. (2009) showed that  
1038 residents, despite having scored lower in novel cage exploration, had a shorter latency to approach a  
1039 novel object, thus being more exploratory regarding curiosity towards a novel object (Mettke-  
1040 Hofmann et al. 2005). Conversely, a within-species study on blue tits reported that migrants were  
1041 the ones to approach the novel object sooner (Nilsson et al. 2010). An explanation for why residents  
1042 were more exploratory towards a novel object is that residents have a stable mental map of their  
1043 environment and the dangers therein, so every new situation can be worth investigating as it may  
1044 represent a new profitable resource or a new threat (Mettke-Hofmann et al. 2009). On the other  
1045 hand, migrants are not bound to an environment and are consistently experiencing new situations,  
1046 so the safest reaction towards a novel object might be to stay away from it and limit their activities  
1047 to well-known and secure situations (Mettke-Hofmann et al. 2009). However, migrants invariably  
1048 find themselves in novel environments when forced to use stopover sites to rest, refuel, or avoid  
1049 storms (Moore and Aborn 2000, Moore et al. 2005). Thus, an explanation for why migrants were  
1050 more exploratory towards a novel object is that migrants need to investigate novel objects to  
1051 acquire the needed knowledge to survive in a new environment (Nilsson et al. 2014), while  
1052 residents by constantly living in the same environment and successfully exploiting the same known  
1053 resources, might be more risk-averse towards a new object, as it can pose a potential danger in an  
1054 otherwise comfortable situation. A different view can be achieved when looking for residents who  
1055 established territory in an urbanized area. Species with more exploratory behavior are generally  
1056 more innovative and more likely to become urbanized (Sol et al. 2002). Innovativeness has been  
1057 shown to relate positively with brain size (Sol et al. 2005), and some studies reported that residents  
1058 had a larger brain size than migrants (Sol et al. 2005, Vincze 2016). This might have been the case  
1059 in elk, where residents living close to human settlements had a lower latency to approach a novel

1060 object than migrants (Found and St. Clair 2016). Areas close to human settlements are highly  
1061 dynamic (Newsome et al. 2015), so a lower latency to approach a novel object can allow residents  
1062 to find novel food opportunities and assess potential new risks.

1063 ***Are migrant groups composed of social individuals?***

1064 Migration is generally a collective movement (Dingle and Drake 2007), and it is no surprise that  
1065 social abilities should be a prerequisite to associate with the migrating group. However, sociability  
1066 was the least studied behavioral trait in my systematic review with only one study. This might  
1067 simply reflect the fact that sociability is the overall least studied behavioral trait with regards to  
1068 species distributions (as I discussed in Chapter One). The only study I found showed that migrants  
1069 were more social than residents (Found and St. Clair 2016). I emphasize the need to conduct further  
1070 research in the link between sociability and partial migration, because contradictory and stimulating  
1071 findings might be possible.

1072 ***Thoughts on behavioral-dependent migration***

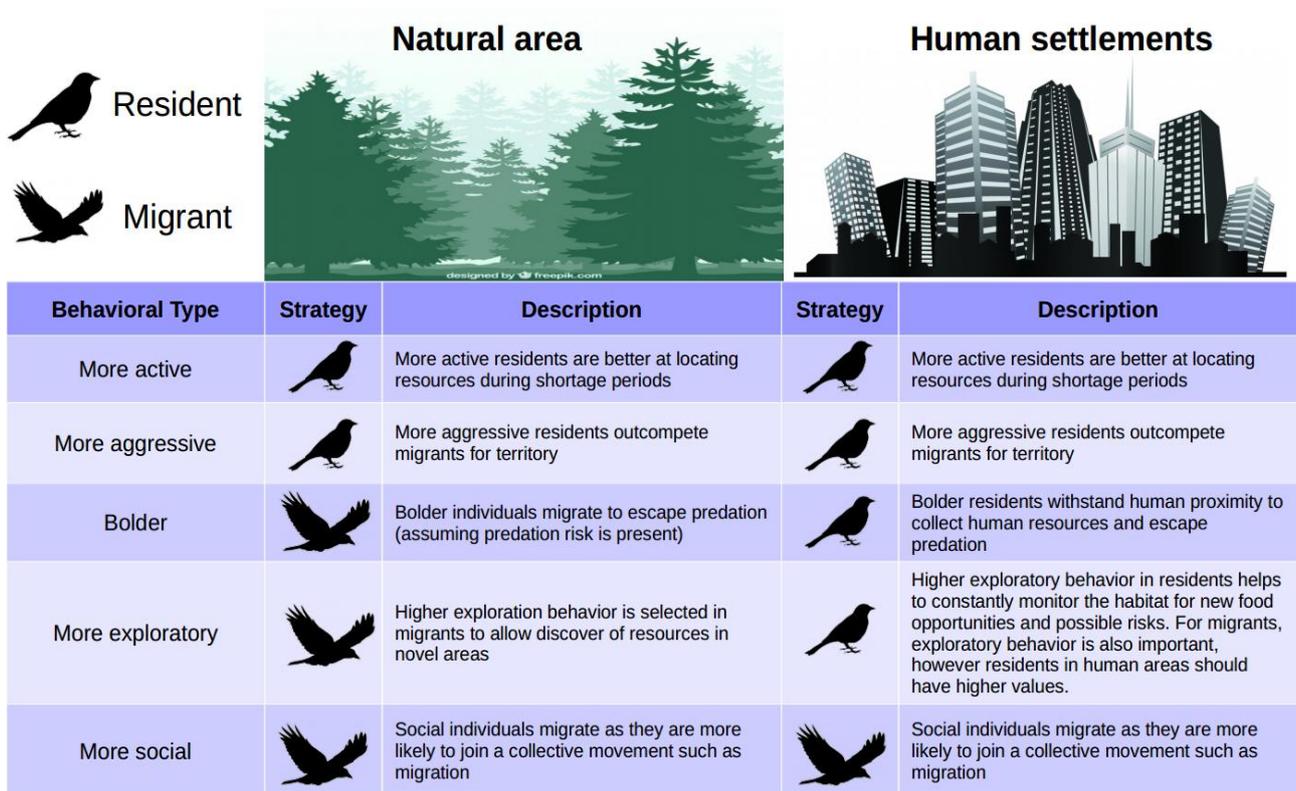
1073 Studying individual differences between migrants and residents can offer great insights about the  
1074 proximate and ultimate causes of migratory tendency. Herein I showed that recent studies assessing  
1075 behavioral-dependent migration found differences in behaviors between those who stay resident and  
1076 those who undergo migration (Nilsson et al. 2010, Chapman et al. 2011b, Warnock and Rasmussen  
1077 2014, Found and St. Clair 2016). Migration or residency can both arise as the most beneficial  
1078 strategy depending on trait specific advantages in the environment, or as the ‘best of a bad job’  
1079 (Chapman et al. 2012). The latter, could enforce residency in individuals with poor body condition  
1080 and lack of energy reserves, or enforce migration in individuals with poor competitive ability to  
1081 acquire resources during periods of shortage in their current environment (Chapman et al. 2012). In  
1082 either case, by making the ‘best of a bad job’ individuals still choose the best strategy to maximize  
1083 their fitness (Chapman et al. 2012). For the former, we can think of behavioral types as part of a

1084 complex set of traits that makes individuals fit to migration in an environmental context, forming  
1085 what is known as a migratory syndrome (Dingle 2006). Individuals displaying the migratory  
1086 syndrome should turn into migrants, while the rest would benefit to choose residency instead.  
1087 Behavioral variation is usually associated with non-behavioral differences (Wolf and Weissing  
1088 2012) which could jointly form a migratory syndrome. For instance, more aggressive individuals  
1089 normally have a larger body size (Edwards and Lailvaux 2013), and more exploratory individuals  
1090 have a larger brain size and are better at learning new tasks (Kotrschal et al. 2014). If behavioral  
1091 traits are the cause or the consequence of non-behavioral variation is difficult to answer, however a  
1092 possibility is that this relation is mutually reinforced through feedback loops (Dall et al. 2004, Wolf  
1093 and Weissing 2012).

1094 For a given population living in an environment characterized by predation risk and seasonal  
1095 shortage of resources, the individuals showing higher levels of activity and aggressiveness might  
1096 possess a competitive advantage over the dispute of resources in periods of scarcity. Furthermore, if  
1097 these same individuals have low levels of boldness to prevent high levels of predator-induced  
1098 mortality, they might be able to stay resident and avoid the costs of migration (Chapman et al.  
1099 2011b). In this context, migrants would migrate because of their innate competitive disadvantage,  
1100 and instead benefit from higher sociability to establish social bonds and cooperate throughout  
1101 migration and from higher exploratory behavior, which could allow a faster search and discovery of  
1102 resources in new environments (Mettke-Hofmann et al. 2009, Nilsson et al. 2010, but see Mettke-  
1103 Hofmann et al. 2005).

1104 Human activity has been a driving force of major ecological changes, leading to an  
1105 unprecedented pace of non-natural environmental disturbance that is disrupting ecological  
1106 opportunities (Hendry et al. 2008, Candolin and Wong 2012). New ecological opportunities are  
1107 found in human proximity areas, sometimes associated with stable food availability and reduced

1108 predation (Chamberlain et al. 2009). However, humans are feared by a vast number of animals and  
 1109 in the case where humans do not predate on animals living in proximity, the individuals who are  
 1110 bold enough to withstand the fear of humans can collect the benefits of low predation and stable  
 1111 food resources. Even though, residency near human settlements could cancel most environmental  
 1112 conditions that might lead to migration (e.g. seasonal scarcity of resources), some individuals have  
 1113 difficulties to cope with human presence and decide to migrate once conditions are favorable to do  
 1114 so (Møller et al. 2013, Found and St. Clair 2016). I argue that when residents live closed to human  
 1115 settlements, they might be bolder in order to withstand human presence, and also more exploratory  
 1116 as they might have to find and experiment with novel resources and risks (Found and St. Clair  
 1117 2016). Because boldness becomes an advantage rather than a disadvantage, this contradicts what we  
 1118 expect when migration happens in natural settings (Figure 2).



**Figure 2** Description of how behavioral differences between residents and migrants, might change if residents stay in natural area (left columns) or if residents stay in proximity to human settlements (right columns). For example, first row shows that individuals with a more active behavioral type are more likely to become residents in natural areas and also more likely to become residents when in close proximity to human settlements.

1119 Human habituation has been linked to declines in migratory tendency (Partecke and Gwinner  
1120 2007, Kirby et al. 2008, White et al. 2014), and despite the importance of behavioral traits to human  
1121 habituation (Ellenberg et al. 2009, Samia et al. 2015), I found only one study explicitly assessing  
1122 behavior and partial migration where residents went through human habituation (Found and St.  
1123 Clair 2016). We should be aware that human habituation is introducing serious challenges such as  
1124 property damage, rise in zoonotic diseases and physical attacks to people (Soulsbury and White  
1125 2015). Interestingly, the resident elk who scored higher on boldness and aggressiveness in Found  
1126 and St. Clair (2016), had a historical record of public safety incidents including one which required  
1127 hospitalization of a person. I remind however that for some threatened migratory species, allowing  
1128 or enforce species' settlement near humans could have the potential to counteract population  
1129 declines.

### 1130 **CONCLUDING REMARKS**

1131 The logistical challenges in the past for studying the relation between behavioral traits and  
1132 migration are becoming buried by recent technological advances that allow cheaper, smaller and  
1133 more effective devices to be used in migration tracking and behavioral analysis (Chapman et al.  
1134 2012, Nilsson et al. 2014, Canestrelli et al. 2016). With these tools at hand, we can start more in-  
1135 depth studies about the proximate and ultimate causes of migration. Specifically, in animal behavior  
1136 research we can try to discern which behavioral types are most likely to migrate according to  
1137 different ecological contexts. I recommend new studies to try to give a better overall picture of  
1138 behavioral-dependent migration by assessing multiple behavioral traits. This could give far better  
1139 insights than multiple studies, studying one or two behavioral traits, on different species and under  
1140 different ecological conditions. I also recommend studies to explicitly assess some factors such as  
1141 predation risk, resource abundance, competition and/or other non-behavioral traits to allow  
1142 encompassing results and the possible determination of general patterns in future meta-analytic  
1143 studies, otherwise difficult to obtain in a single primary study. I am not aware of any study

1144 evaluating behavioral changes in residents and migrants throughout a migratory cycle. If residents  
1145 and migrants live temporarily in sympatry, residents can be more aggressive and territorial when  
1146 migrants arrive and density is high but relax this behavior once migrants depart and density  
1147 decreases. Also, because of the physiological changes conferring migrants the ‘superpowers’ needed  
1148 to undergo migration, migrants could display higher activity levels if caught while migrating.

1149 I point out that in my systematic review, only one study evaluated the link between behavior,  
1150 human habituation and residency and I argue that this link merits further research. In doing so, one  
1151 could assess the extent of possible shifts in migratory behavior attributed to anthropogenic factors.  
1152 Human-induced rapid environmental changes are taking their toll on migratory species, and unless  
1153 species are fast enough to adapt, they can succumb along with all their ecological interactions. Even  
1154 if species persist but migration behavior is lost, such a change can have tremendous effects on  
1155 species that depend on migratory journeys for predation, parasitism, competition and mutualism.  
1156 Migratory tendency is driven by the interplay of different factors in specific environmental  
1157 contexts, so understanding which factors are important in each context could advance our  
1158 knowledge of what conditions must be kept to protect migratory journeys and all species that rely  
1159 on them. Ultimately this includes many human families around the world that depend on animal  
1160 migratory paths to acquire food and money to survive.

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1284 **APPENDIX A. *Details on literature search***

1285

1286 **Web of Science**

1287

1288 I searched in Web of Science database for studies published before 15 June 2016 and written in  
1289 English. Due to a wide terminology in animal personality research, I used an extensive list of terms  
1290 attempting to detect most of the relevant studies:

1291 ((personalit\* OR temperament OR "behavi?ral type\*" OR "individual differences" OR  
1292 "individual variation" OR "intraspecific variation" OR "behavi?ral phenotype" OR "behavi?ral  
1293 strategies" OR "behavi?ral syndromes" OR "behavi?ral differences" OR "behavi?ral trait\*" OR  
1294 "behavi?ral flexibility" OR "behavi?ral polymorphism") OR (bold\* OR "risk taking" OR fear\*) OR  
1295 (aggress\*) OR (explorat\* OR neoph\*) OR (socia\* AND behav\*) OR (activ\* AND behav\*)) AND  
1296 (animal\* OR species OR fish\* OR amphibian\* OR reptil\* OR bird\* OR mammal\* OR insect\*)  
1297 AND (dispers\* OR invasi\* OR migrat\* OR "range expansion" OR introduction OR departure OR  
1298 transience OR establish\* OR settle\*)

1299 Since some terms may be used interchangeably between different research areas (e.g. activity can  
1300 be used as foraging activity or as geothermal activity), I narrowed the scope of some terms (e.g  
1301 (activ\* AND behav\*)). I also added a set of terms limiting the search to just those studies that refer  
1302 to animals or species.

1303 The search returned over 90000 records, from a multitude of research areas. To reduce this  
1304 number to a workable quantity I used Web of Science refining procedures. I examined known  
1305 studies, which assess animal personalities' effects on species distributions, for their registered  
1306 research areas. As a result, I refined records to include the following research areas:

1307 Environmental Sciences Ecology OR Zoology OR Behavioral Sciences OR Marine Freshwater  
1308 Biology OR Science Technology Other Topics OR Life Sciences Biomedicine Other Topics OR

1309 Entomology OR Evolutionary Biology OR Oceanography OR Biodiversity Conservation OR  
1310 Endocrinology Metabolism.

1311 The refined search turned up 14090 studies. I considered the search accurate after searched for and  
1312 confirmed the presence of the following studies: Duckworth and Badyaev 2007, Pintor et al. 2008,  
1313 Mettke-Hofmann et al. 2009, Cote et al. 2010b, Chapman et al. 2011b, Chapple et al. 2011, Liebl and  
1314 Martin 2012, Brodin et al. 2013, Hudina et al. 2015, Myles-Gonzalez et al. 2015.

1315 Although restricting the search might have excluded some relevant studies, I argue that my  
1316 extensive search not limited by Web of Science records, will have the capacity to retrieve almost all  
1317 relevant studies conducted so far.

1318

### 1319 **Google Scholar**

1320 Google Scholar database is a good source to look for grey literature, journals not available on  
1321 Web of Science, and more recent studies not updated in other databases.

1322 I conducted the Google Scholar search between 15 and 17 June 2016, using nine sets of terms:

1323 1) personality migrat\* animal OR species

1324 2) personality invasi\* animal OR species

1325 3) personality dispers\* animal OR species

1326 4) temperament migrat\* animal OR species

1327 5) temperament invasi\* animal OR species

1328 6) temperament dispers\* animal OR species

1329 7) behavior migrat\* animal OR species

1330 8) behavior invasi\* animal OR species

1331 9) behavior dispers\* animal OR species

1332

1333 Each set of terms was searched twice, once for all years and once for studies published after

1334 2015. The latter allowed me to retrieve recent literature absent in Web of Science database.

1335 I ordered search results by relevance and collected the first 100 records in each search. All

1336 Google Scholar searches summed up to 1800 studies. A visual inspection on these studies

1337 confirmed that this method allowed me to incorporate some grey literature (e.g. thesis) and recent

1338 literature absent from Web of Science search.

1339

### 1340 **Combining Web of Science and Google Scholar records**

1341 I combined the records from Web of Science and Google scholar databases (total of 15890

1342 studies) and removed 377 duplicates with *EndNote* software. The remaining 15513 studies were

1343 imported to *abstrackr* to be screened by title and abstract.

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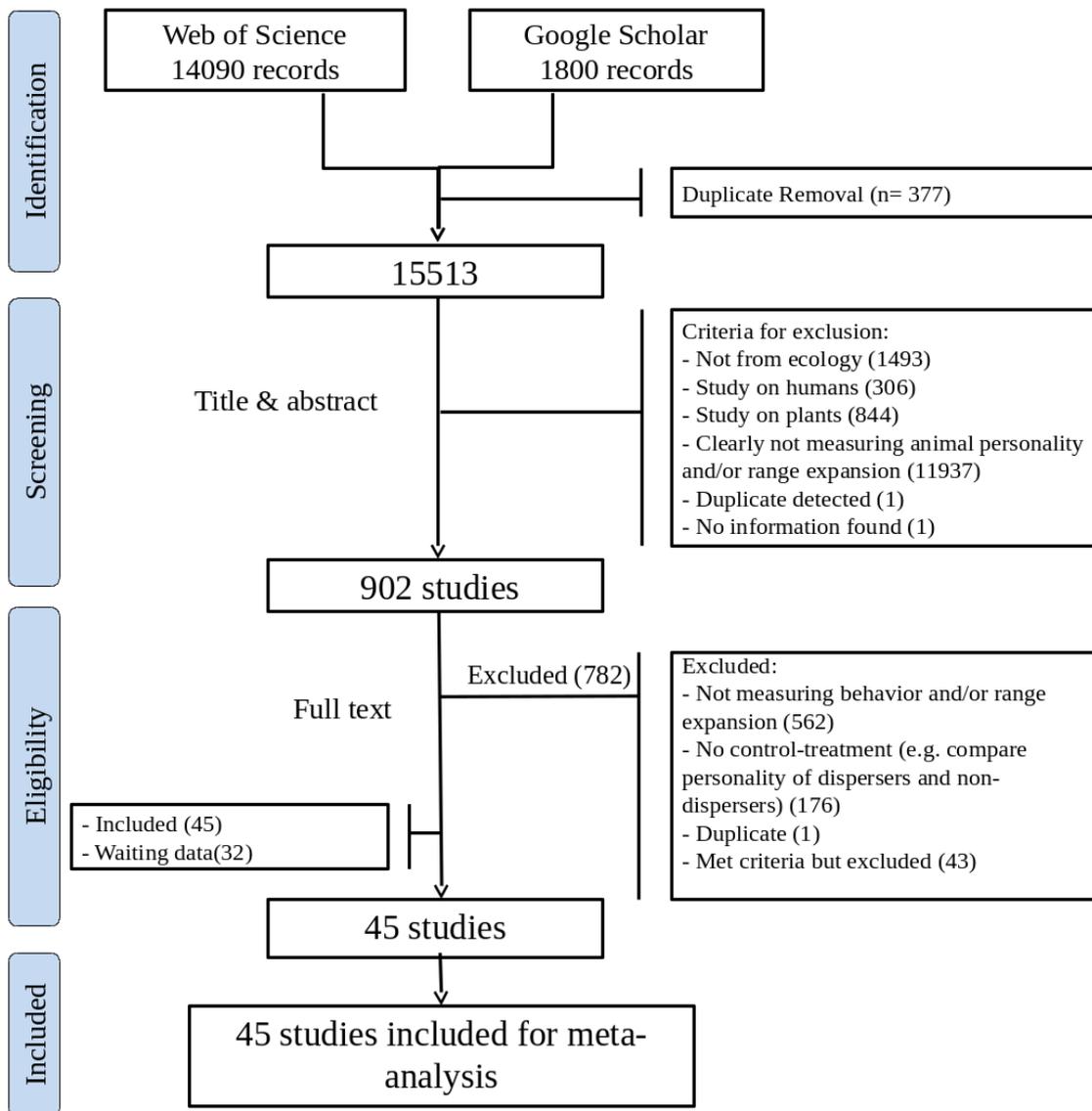
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1353 **APPENDIX B. PRISMA Diagram**

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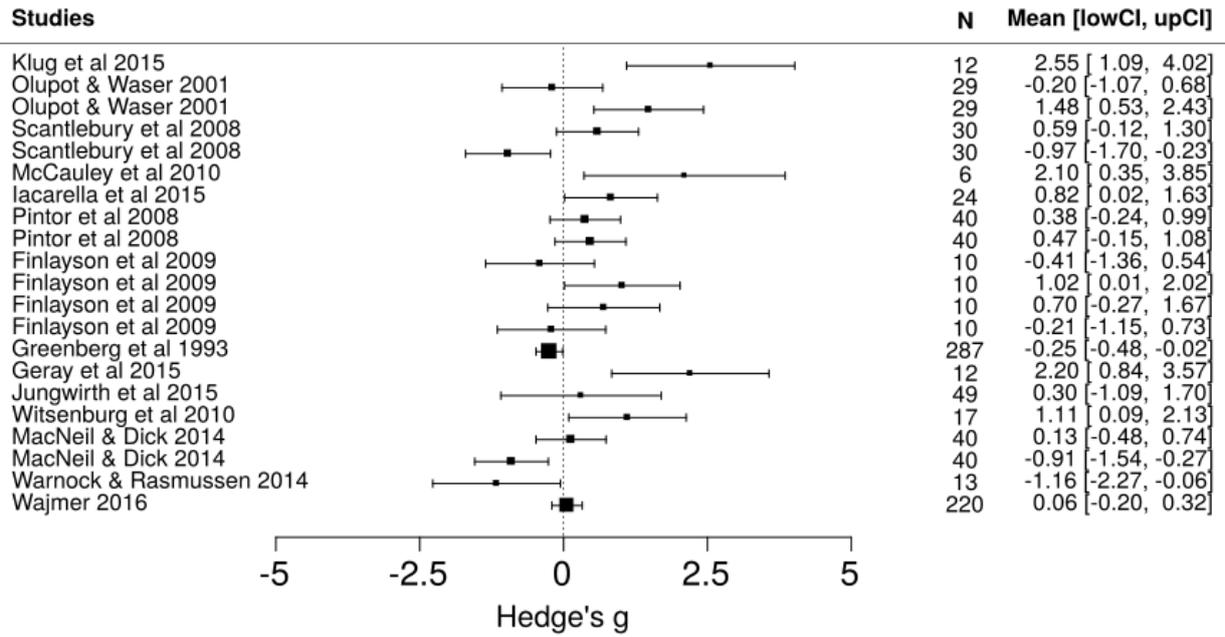


Met criteria but excluded means a study passed the inclusion criteria, however it lacked some features needed to conduct meta-analysis (e.g. no species-specific data; or study design allowing for residency effects in behavioral assessments). Waiting data means contact was made with the author in order to obtain missing data needed to calculate the effect size, but no response was yet obtained.

1396 **APPENDIX C. Forests Plots**

1397 **Activity**

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1399 **Figure 1** Forest plot for the behavioral trait activity. Square sizes are related to effect size precision with bigger sizes  
 1400 representing higher precision. Studies are written as: AuthorsYear. N is the effect size sample size. lowCI and uppCI are  
 1401 respectively the lower and upper 95% confidence interval.

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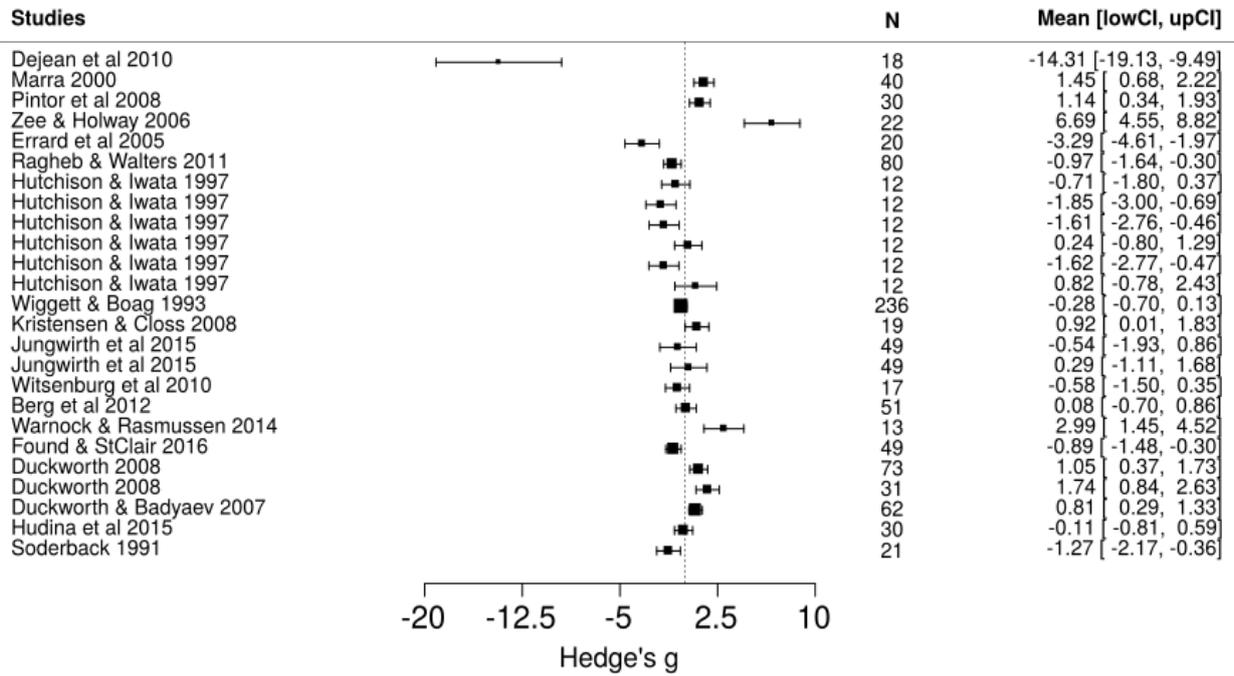
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1409 **Aggressiveness**

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1412 **Figure 2** Forest plot for the behavioral trait aggressiveness. Square sizes are related to effect size precision with bigger  
 1413 sizes representing higher precision. Studies are written as: AuthorsYear. N is the effect size sample size. lowCI and  
 1414 uppCI are respectively the lower and upper 95% confidence interval.

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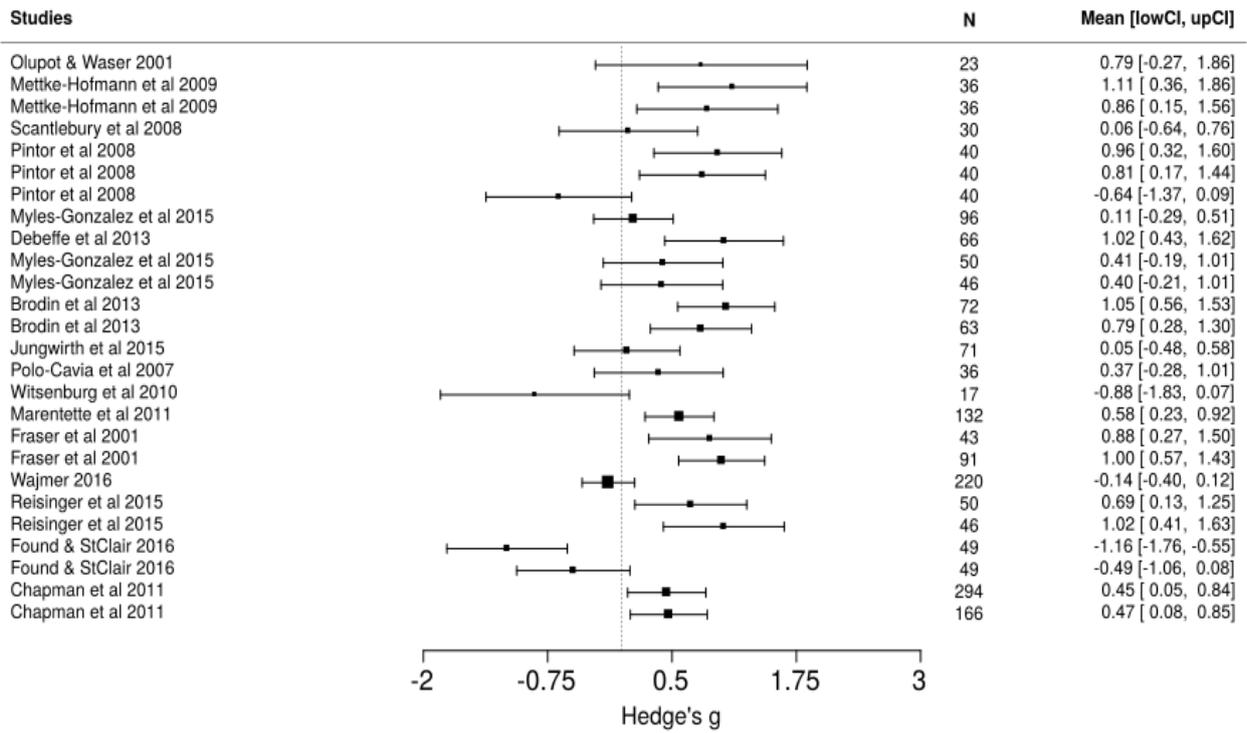
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1422 **Boldness**

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1424 **Figure 3** Forest plot for the behavioral trait boldness. Square sizes are related to effect size precision with bigger sizes  
 1425 representing higher precision. Studies are written as: AuthorsYear. N is the effect size sample size. lowCI and uppCI are  
 1426 respectively the lower and upper 95% confidence interval.

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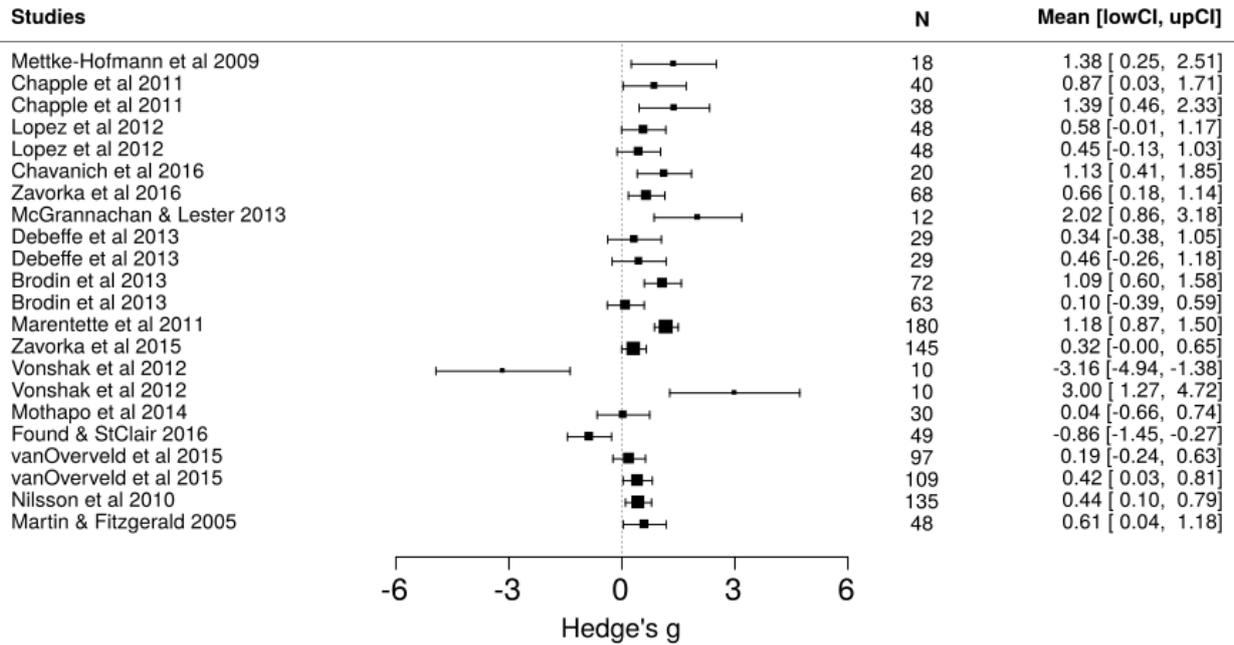
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1435 **Exploratory**

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1437 **Figure 4** Forest plot for the behavioral trait exploratory. Square sizes are related to effect size precision with bigger  
 1438 sizes representing higher precision. Studies are written as: AuthorsYear. N is the effect size sample size. lowCI and  
 1439 uppCI are respectively the lower and upper 95% confidence interval.

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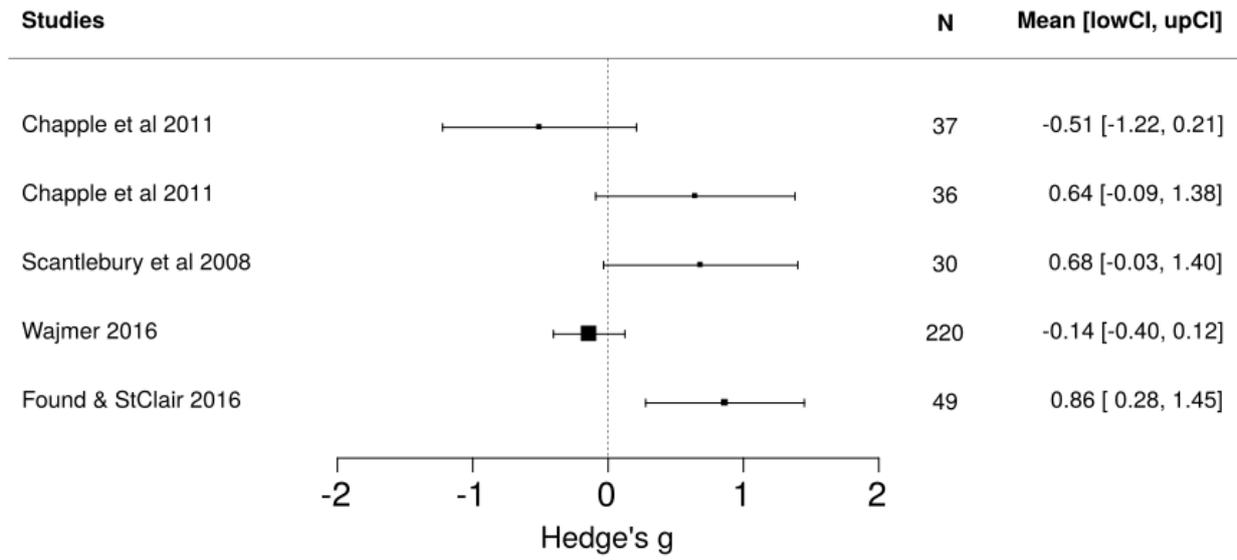
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1449 **Sociability**

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1451 **Figure 5** Forest plot for the behavioral trait sociability. Square sizes are related to effect size precision with bigger sizes  
 1452 representing higher precision. Studies are written as: AuthorsYear. N is the effect size sample size. lowCI and uppCI are  
 1453 respectively the lower and upper 95% confidence interval.

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1464 **APPENDIX D. Table of studies**

1465 **Table 1** Number of entries per study in each behavioral trait, and total sums of entries and studies per behavioral trait in  
 1466 the two last rows

Study reference	Activity	Aggressiveness	Boldness	Exploratory	Sociability
Berg et al 2012	0	1	0	0	0
Brodin et al 2013	0	0	2	2	0
Chapman et al 2011	0	0	2	0	0
Chapple et al 2011	0	0	0	2	2
Chavanich et al 2016	0	0	0	1	0
Debeffe et al 2013	0	0	1	2	0
Dejean et al 2010	0	1	0	0	0
Duckworth & Badyaev 2007	0	1	0	0	0
Duckworth 2008	0	2	0	0	0
Errard et al 2005	0	1	0	0	0
Finlayson et al 2009	4	0	0	0	0
Found & StClair 2016	0	1	2	1	1
Fraser et al 2001	0	0	2	0	0
Geray et al 2015	1	0	0	0	0
Greenberg et al 1993	1	0	0	0	0
Hudina et al 2015	0	1	0	0	0
Hutchison & Iwata 1997	0	6	0	0	0
Iacarella et al 2015	1	0	0	0	0
Jungwirth et al 2015	1	2	1	0	0
Klug et al 2015	1	0	0	0	0
Kristensen & Closs 2008	0	1	0	0	0
Lopez et al 2012	0	0	0	2	0
MacNeil & Dick 2014	2	0	0	0	0
Marentette et al 2011	0	0	1	1	0
Marra 2000	0	1	0	0	0
Martin & Fitzgerald 2005	0	0	0	1	0
McCauley et al 2010	1	0	0	0	0
McGrannachan & Lester 2013	0	0	0	2	0
Mettke-Hofmann et al 2009	0	0	2	1	0
Mothapo et al 2014	0	0	0	1	0
Myles-Gonzalez et al 2015	0	0	3	0	0
Nilsson et al 2010	0	0	0	1	0
Olupot & Waser 2001	2	0	1	0	0
Pintor et al 2008	2	1	3	0	0

Polo-Cavia et al 2008	0	0	1	0	0
Ragheb & Walters 2011	0	1	0	0	0
Reisinger et al 2015	0	0	2	0	0
Scantlebury et al 2008	2	0	1	0	1
Soderback 1991	0	1	0	0	0
Van Overveld et al 2015	0	0	0	2	0
Vonshak et al 2012	0	0	0	2	0
Wajmer 2016	1	0	1	0	1
Warnock & Rasmussen 2014	1	1	0	0	0
Wiggett & Boag 1993	0	1	0	0	0
Witsenburg et al 2010	1	1	1	0	0
Zavorka et al 2015	0	0	0	1	0
Zavorka et al 2016	0	0	0	1	0
Zee & Holway 2006	0	1	0	0	0
Total entries/behavioral trait	21	25	26	22	5
Total studies/behavioral trait	14	18	16	16	4

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1596 **APPENDIX E. Results from models**

1597 **Hierarchical model with study random effects (no moderators)**

1598 **Table 1** Statistics obtained from the posterior distribution of the summary effect size in a hierarchical model with effect  
 1599 sizes nested within studies. SD is the standard deviation and 95% CI are the 95% credible intervals. Prob > 0 is the  
 1600 probability that a behavioral trait had an effect size value higher than zero over all MCMC iterations. DIC is the  
 1601 Deviance Information Criterion. N relates to the number of studies or entries.

Behavioral Trait	Mean	SD	95% CI	Prob > 0	DIC	N (Studies/Entries)
Activity	0.4332	0.2685	[-0.0560 , 1.0100]	0.9603	80.9	14 / 21
Aggressiveness	-0.1290	1.0208	[-1.694 , 1.335]	0.4352	85.7	18 / 25
Boldness	0.3867	0.1570	[0.0720 , 0.6967]	0.9901	30.1	16 / 26
Exploratory	0.5822	0.1563	[0.2745 , 0.8975]	0.9993	69.2	16 / 22
Sociability	0.3188	0.8168	[-0.8769 , 1.5990]	0.8062	9.5	4 / 5

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1603 **Hierarchical model with biogeographical processes as moderator**

1604 **Activity**

1605 **Table 2** Statistics obtained for activity from the posterior distribution of the summary effect size in a hierarchical model  
 1606 with effect sizes nested within studies and biogeographical process as moderator. SD is the standard deviation and 95%  
 1607 CI are the 95% credible intervals. Prob > 0 is the probability that a behavioral trait had an effect size value higher than  
 1608 zero over all MCMC iterations. DIC is the Deviance Information Criterion. N relates to the number of studies or entries.

Activity	Mean	SD	95% CI	Prob > 0	N (Studies / Entries)
Dispersal	0.4993	0.4436	[-0.3485 , 1.4170]	0.8854	6 / 8
Invasion	0.6316	0.4209	[-0.1348 , 1.5440]	0.9495	6 / 11
Migration	-	-	-	-	2 / 2

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1610 **Aggressiveness**

1611 **Table 3** Statistics obtained for aggressiveness from the posterior distribution of the summary effect size in a hierarchical  
 1612 model with effect sizes nested within studies and biogeographical process as moderator. SD is the standard deviation and  
 1613 95% CI are the 95% credible intervals. Prob > 0 is the probability that a behavioral trait had an effect size value higher  
 1614 than zero over all MCMC iterations. DIC is the Deviance Information Criterion. N relates to the number of studies or  
 1615 entries.

Aggressiveness	Mean	SD	95% CI	Prob > 0	N (Studies / Entries)
Dispersal	0.0134	1.3380	[-2.694 , 2.687]	0.5068	7 / 9
Invasion	-1.1455	1.5180	[-4.275 , 1.773]	0.2128	6 / 6
Migration	0.6515	1.5671	[-2.457 , 3.822]	0.6725	5 / 10

1616 **Boldness**

1617 **Table 4** Statistics obtained for boldness from the posterior distribution of the summary effect size in a hierarchical  
 1618 model with effect sizes nested within studies and biogeographical process as moderator. SD is the standard deviation and 95%  
 1619 CI are the 95% credible intervals. Prob > 0 is the probability that a behavioral trait had an effect size value higher than  
 1620 zero over all MCMC iterations. DIC is the Deviance Information Criterion. N relates to the number of studies or entries.

Boldness	Mean	SD	95% CI	Prob > 0	N (Studies / Entries)
Dispersal	0.4228	0.2353	[-0.0544 , 0.8846]	0.9620	9 / 11
Invasion	0.4811	0.3237	[-0.1660 , 1.1270]	0.9354	4 / 9
Migration	0.1950	0.3743	[-0.5484 , 0.9478]	0.7117	3 / 6

1621 **Exploratory**

1622 **Table 5** Statistics obtained for exploratory from the posterior distribution of the summary effect size in a hierarchical  
 1623 model with effect sizes nested within studies and biogeographical process as moderator. SD is the standard deviation and  
 1624 95% CI are the 95% credible intervals. Prob > 0 is the probability that a behavioral trait had an effect size value higher  
 1625 than zero over all MCMC iterations. DIC is the Deviance Information Criterion. N relates to the number of studies or  
 1626 entries.

Exploratory	Mean	SD	95% CI	Prob > 0	N (Studies / Entries)
Dispersal	0.5446	0.2546	[0.0253 , 1.0560]	0.9789	6 / 9
Invasion	0.7332	0.2701	[0.1972 , 1.2760]	0.9933	7 / 10
Migration	-	-	-	-	3 / 3

1627 **Hierarchical model with taxonomic class of the studied individuals as moderator**

1628 **Activity**

1629 **Table 6** Statistics obtained for activity from the posterior distribution of the summary effect size in a hierarchical model  
 1630 with effect sizes nested within studies and taxonomic class as moderator. SD is the standard deviation and 95% CI are the  
 1631 95% credible intervals. Prob > 0 is the probability that a behavioral trait had an effect size value higher than zero over all  
 1632 MCMC iterations. DIC is the Deviance Information Criterion. N relates to the number of studies or entries.

Activity	Mean	SD	95% CI	Prob > 0	N (Studies / Entries)
Actinopterygii	0.4396	0.6265	[-0.7815 , 1.6920]	0.7910	5 / 5
Aves	-	-	-	-	1 / 1
Insecta	0.8194	0.9237	[-0.8670 , 2.8270]	0.8506	2 / 5
Malacostraca	0.2400	0.7155	[-1.1580 , 1.7240]	0.6562	3 / 5
Mammalia	-	-	-	-	2 / 4
Reptilia	-	-	-	-	1 / 1

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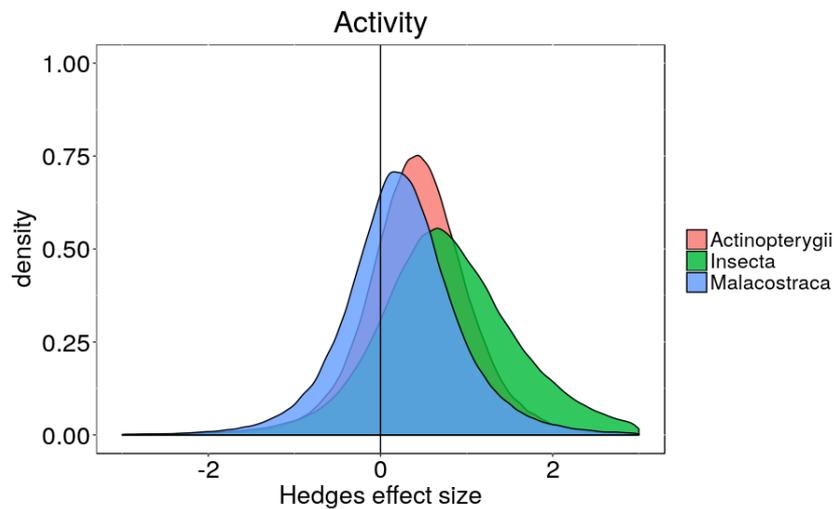
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**Figure 1** Posterior Distribution of activity for taxonomic class as moderator

1649 **Aggressiveness**

1650 **Table 7** Statistics obtained for aggressiveness from the posterior distribution of the summary effect size in a hierarchical  
 1651 model with effect sizes nested within studies and taxonomic class as moderator. SD is the standard deviation and 95% CI  
 1652 are the 95% credible intervals. Prob > 0 is the probability that a behavioral trait had an effect size value higher than zero  
 1653 over all MCMC iterations. DIC is the Deviance Information Criterion. N relates to the number of studies or entries.

Aggressiveness	Mean	SD	95% CI	Prob > 0	N (Studies / Entries)
Actinopterygii	0.2104	0.7514	[-1.1910 , 1.801]	0.6050	5 / 11
Aves	0.7140	0.8311	[-0.9671 , 2.369]	0.8323	4 / 5
Insecta	-	-	-	-	4 / 4
Malacostraca	-	-	-	-	3 / 3
Mammalia	-	-	-	-	2 / 2

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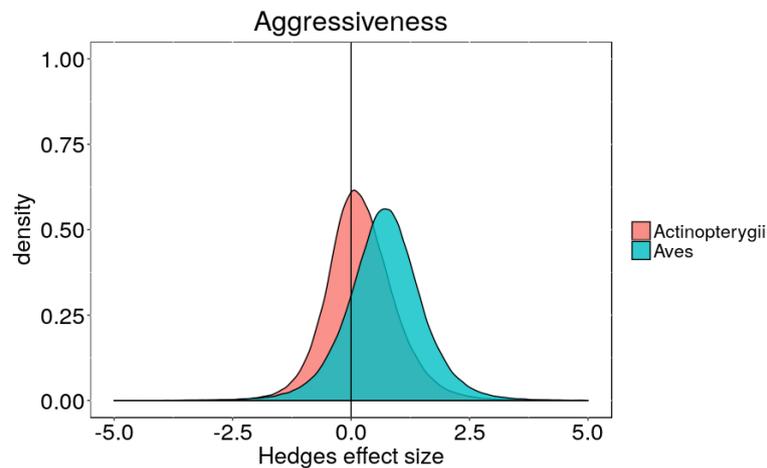
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**Figure 2** Posterior Distribution of aggressiveness for taxonomic class as moderator

1672 **Boldness**

1673 **Table 8** Statistics obtained for boldness from the posterior distribution of the summary effect size in a hierarchical model  
 1674 with effect sizes nested within studies and taxonomic class as moderator. SD is the standard deviation and 95% CI are the  
 1675 95% credible intervals. Prob > 0 is the probability that a behavioral trait had an effect size value higher than zero over all  
 1676 MCMC iterations. DIC is the Deviance Information Criterion. N relates to the number of studies or entries.

Boldness	Mean	SD	95% CI	Prob > 0	N (Studies / Entries)
Actinopterygii	0.2645	0.2669	[-0.2922 , 0.7787]	0.8554	7 / 11
Amphibia	-	-	-	-	1 / 2
Aves	-	-	-	-	1 / 2
Malacostraca	0.6341	0.4618	[-0.2811 , 1.5740]	0.9245	2 / 5
Mammalia	0.1342	0.3867	[-0.6024 , 0.9354]	0.6368	4 / 5
Reptilia	-	-	-	-	1 / 1

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**Figure 3** Posterior Distribution of boldness for taxonomic class as moderator

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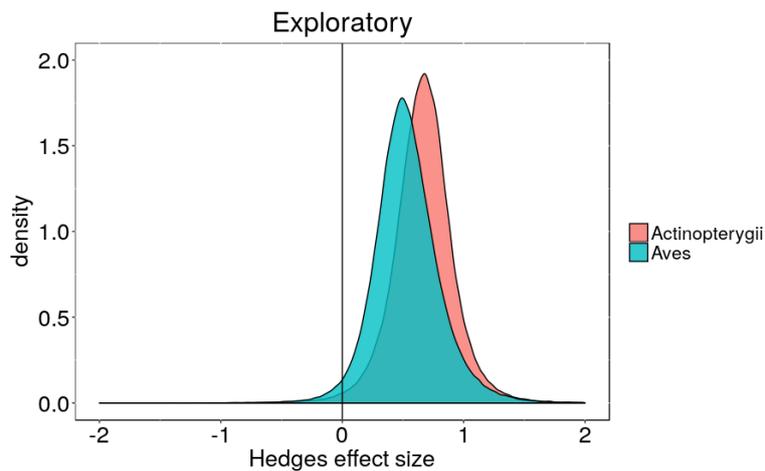
1694 **Exploratory**

1695 **Table 9** Statistics obtained for exploratory from the posterior distribution of the summary effect size in a hierarchical  
 1696 model with effect sizes nested within studies and taxonomic class as moderator. SD is the standard deviation and 95% CI  
 1697 are the 95% credible intervals. Prob > 0 is the probability that a behavioral trait had an effect size value higher than zero  
 1698 over all MCMC iterations. DIC is the Deviance Information Criterion. N relates to the number of studies or entries.

Exploratory	Mean	SD	95% CI	Prob > 0	N (Studies / Entries)
Actinopterygii	0.6677	0.2578	[0.1503 , 1.1780]	0.9888	4 / 5
Amphibia	-	-	-	-	1 / 2
Aves	0.5347	0.2761	[0.0292 , 1.1290]	0.9794	4 / 5
Insecta	-	-	-	-	3 / 4
Malacostraca	-	-	-	-	1 / 1
Mammalia	-	-	-	-	2 / 3
Reptilia	-	-	-	-	1 / 2

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**Figure 4** Posterior Distribution of exploratory for taxonomic class as moderator

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1715 **Hierarchical model with type of behavioral measurements as moderator**

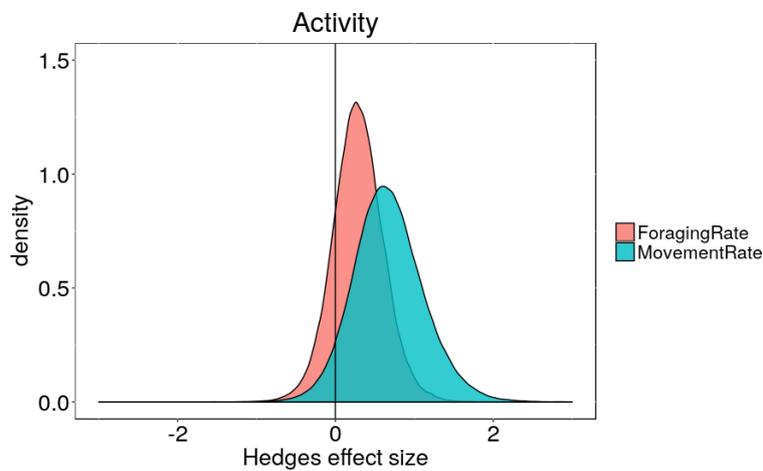
1716 **Activity**

1717 **Table 10** Statistics obtained for activity from the posterior distribution of the summary effect size in a hierarchical  
 1718 model with effect sizes nested within studies and behavioral measurement as moderator. SD is the standard deviation  
 1719 and 95% CI are the 95% credible intervals. Prob > 0 is the probability that a behavioral trait had an effect size value  
 1720 higher than zero over all MCMC iterations. N relates to the number of studies or entries.

Activity	Mean	SD	95% CI	Prob > 0	N (Studies / Entries)
Foraging Rate	0.2872	0.3247	[-0.3468 , 0.9448]	0.8236	11 / 14
Movement Rate	0.6724	0.4460	[-0.1599, 1.6100]	0.9448	6 / 7

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**Figure 5** Posterior Distributions of activity with behavioral measurement as moderator

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1732 **Aggressiveness**

1733 **Table 11** Number of studies and entries for the moderator levels of behavioral measurement in the behavioral trait  
 1734 aggressiveness. Model were not performed because of low sample size for all levels but “Confront w/ intraspecific”

Moderator Level	Studies	Entries
Confront w/ intraspecific	12	16
Confront w/ interspecific	3	3
Confront w/ intraspecific model	2	3
Confront w/ interspecific model	1	1
Social rank	2	2

1736 **Boldness**

1737 **Table 12** Statistics obtained for boldness from the posterior distribution of the summary effect size in a hierarchical  
 1738 model with effect sizes nested within studies and behavioral measurement as moderator. SD is the standard deviation  
 1739 and 95% CI are the 95% credible intervals. Prob > 0 is the probability that a behavioral trait had an effect size value  
 1740 higher than zero over all MCMC iterations. N relates to the number of studies or entries.

<b>Boldness</b>	<b>Mean</b>	<b>SD</b>	<b>95% CI</b>	<b>Prob &gt; 0</b>	<b>N (Studies / Entries)</b>
<b>Latency to Enter Novel Area</b>	0.5401	0.2300	[0.0859 , 1.0020]	0.9878	9 / 14
<b>Latency to Forage under Risk</b>	-	-	-	-	1 / 2
<b>Latency to Move under Risk</b>	-	-	-	-	2 / 2
<b>Response to Threat</b>	-0.3590	0.3754	[-1.1290 , 0.3600]	0.1567	4 / 5
<b>Scanning</b>	-	-	-	-	3 / 3

1741 **Exploratory**

1742 **Table 13** Statistics obtained for exploratory from the posterior distribution of the summary effect size in a hierarchical  
 1743 model with effect sizes nested within studies and behavioral measurement as moderator. SD is the standard deviation  
 1744 and 95% CI are the 95% credible intervals. Prob > 0 is the probability that a behavioral trait had an effect size value  
 1745 higher than zero over all MCMC iterations. N relates to the number of studies or entries.

<b>Exploratory</b>	<b>Mean</b>	<b>SD</b>	<b>95% CI</b>	<b>Prob &gt; 0</b>	<b>N (Studies / Entries)</b>
<b>Exploration of Novel Area</b>	0.6050	0.2244	[0.1577 , 1.0640]	0.9927	9 / 13
<b>Find Resource in Novel Area</b>	0.8490	0.3743	[0.0951 , 1.5860]	0.9844	5 / 6
<b>Reaction to Novel Object or Food</b>	-	-	-	-	3 / 3

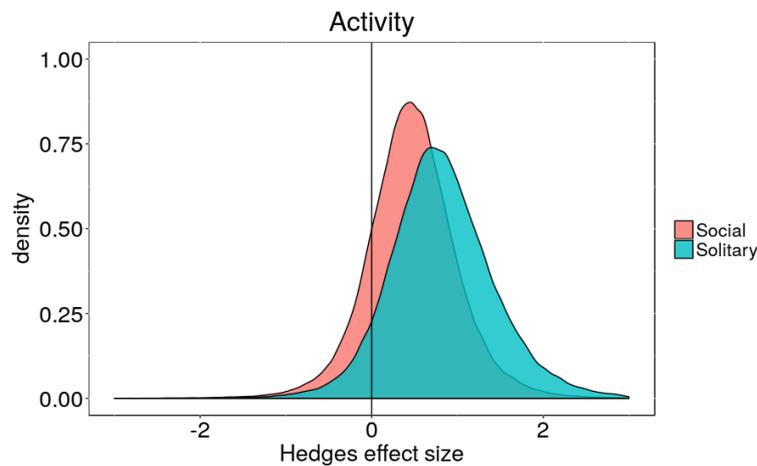
1746 **Hierarchical model with social organization of the studied species as moderator**

1747 *Activity*

1748 **Table 14** Statistics obtained for activity from the posterior distribution of the summary effect size in a hierarchical  
 1749 model with effect sizes nested within studies and social organization as moderator. SD is the standard deviation and  
 1750 95% CI are the 95% credible intervals. Prob > 0 is the probability that a behavioral trait had an effect size higher  
 1751 than zero over all MCMC iterations. N relates to the number of studies or entries.

Activity	Mean	SD	95% CI	Prob > 0	N (Studies / Entries)
Partly Social	-	-	-	-	1 / 4
Social	0.4717	0.5336	[-0.5748 , 1.5690]	0.8399	5 / 7
Solitary	0.8258	0.6278	[-0.3356 , 2.1630]	0.9278	4 / 5

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**Figure 6** Posterior Distributions for activity with social organization as moderator

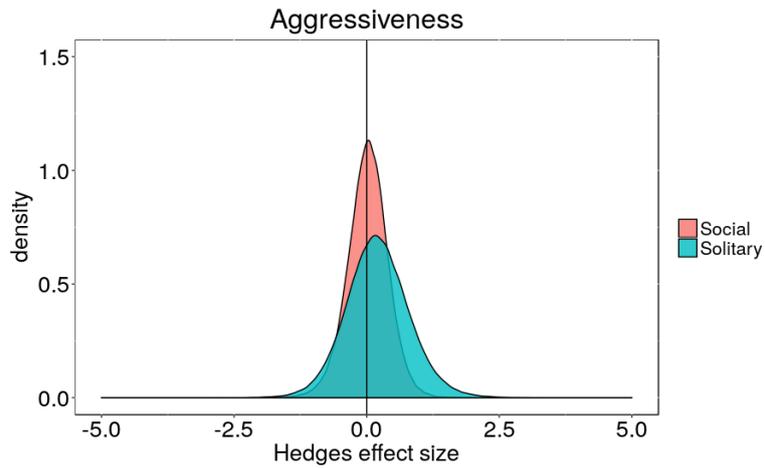
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1761 *Aggressiveness*

1762 **Table 15** Statistics obtained for aggressiveness from the posterior distribution of the summary effect size in a  
 1763 hierarchical model with effect sizes nested within studies and social organization as moderator. SD is the standard  
 1764 deviation and 95% CI are the 95% credible intervals. Prob > 0 is the probability that a behavioral trait had an effect size  
 1765 value higher than zero over all MCMC iterations. N relates to the number of studies or entries.

Aggressiveness	Mean	SD	95% CI	Prob > 0	N (Studies / Entries)
Eusocial	-	-	-	-	3 / 3
Partly Social	-	-	-	-	1 / 1
Social	0.0174	0.3830	[-0.7679 , 0.7582]	0.5288	10 / 12
Solitary	0.2053	0.5973	[-0.9475 , 1.4260]	0.6357	4 / 5

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**Figure 7** Posterior Distributions for aggressiveness with social organization as moderator

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1768 **Boldness**

1769 **Table 16** Statistics obtained for boldness from the posterior distribution of the summary effect size in a hierarchical  
 1770 model with effect sizes nested within studies and social organization as moderator. SD is the standard deviation and  
 1771 95% CI are the 95% credible intervals. Prob > 0 is the probability that a behavioral trait had an effect size value higher  
 1772 than zero over all MCMC iterations. N relates to the number of studies or entries.

Boldness	Mean	SD	95% CI	Prob > 0	N (Studies / Entries)
Partly Social	0.5810	0.3586	[-0.1270 , 1.3100]	0.9522	3 / 6
Social	0.0825	0.2613	[-0.4386 , 0.6063]	0.6338	7 / 9
Solitary	0.7638	0.3519	[0.0595 , 1.4750]	0.9812	3 / 7

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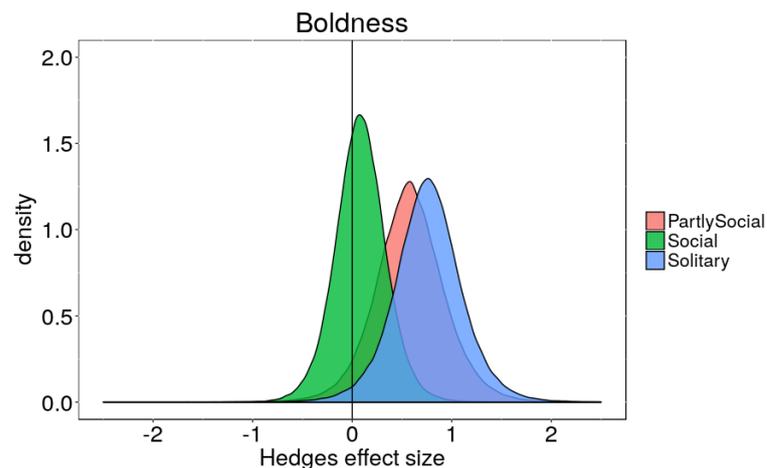
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**Figure 8** Posterior Distributions for boldness with social organization as moderator

1783 **Exploratory**

1784 **Table 17** Number of studies and entries for the moderator levels of social organization in the behavioral trait  
 1785 exploratory. Model were not performed because of low sample size for all levels but “Social”

Moderator Level	Studies	Entries
Eusocial	3	4
Partly Social	2	2
Social	8	11
Solitary	1	2

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1787 **Hierarchical models with type of study design as moderator**

1788 **Activity**

1789 **Table 18** Statistics obtained for activity from the posterior distribution of the summary effect size in a hierarchical  
 1790 model with effect sizes nested within studies and study design as moderator. SD is the standard deviation and 95% CI  
 1791 are the 95% credible intervals. Prob > 0 is the probability that a behavioral trait had an effect size value higher than zero  
 1792 over all MCMC iterations. N relates to the number of studies or entries.

Activity	Mean	SD	95% CI	Prob > 0	N (Studies / Entries)
Experimental	0.4177	0.3405	[-0.2303 , 1.1290]	0.9052	9 / 14
Observational	0.4209	0.4667	[-0.4760 , 1.3830]	0.8314	5 / 7

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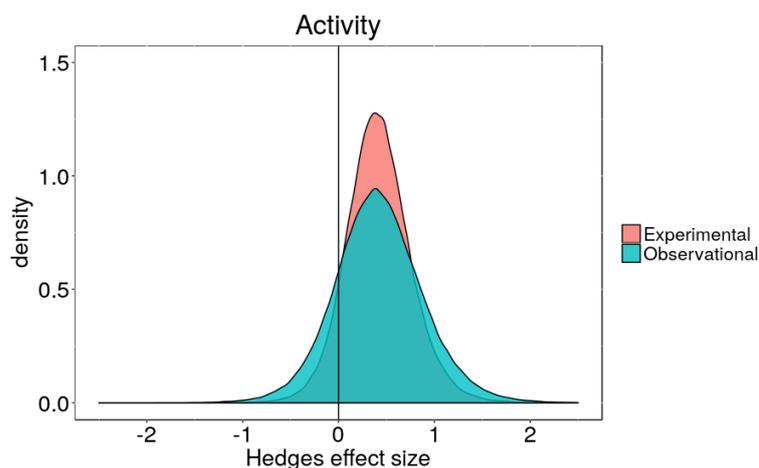
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**Figure 9** Posterior Distributions for activity with study design as moderator

1805 **Aggressiveness**

1806 **Table 19** Statistics obtained for aggressiveness from the posterior distribution of the summary effect size in a  
 1807 hierarchical model with effect sizes nested within studies and study design as moderator. SD is the standard deviation  
 1808 and 95% CI are the 95% credible intervals. Prob > 0 is the probability that a behavioral trait had an effect size value  
 1809 higher than zero over all MCMC iterations. N relates to the number of studies or entries.

Aggressiveness	Mean	SD	95% CI	Prob > 0	N (Studies / Entries)
Experimental	-0.5098	0.8905	[-2.3610 , 1.1890]	0.2756	14 / 20
Observational	1.1545	1.6455	[-2.1010 , 4.5120]	0.7732	4 / 5

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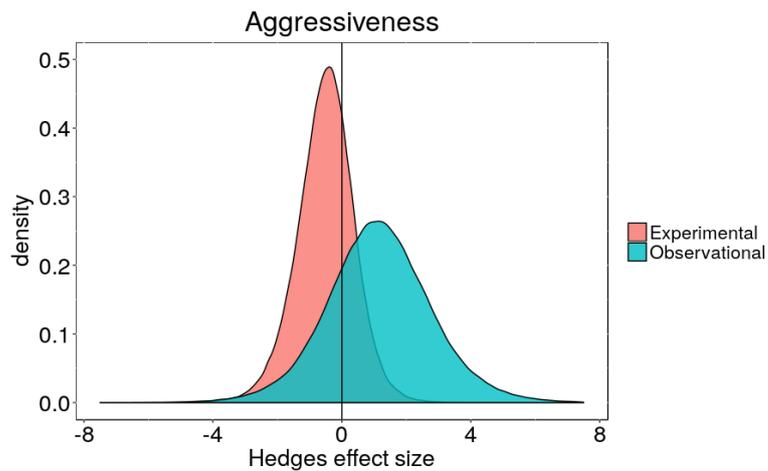
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**Figure 10** Posterior Distributions for activity with study design as moderator

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1820 **Table 20** Table showing the number of studies and entries per behavioral trait and study type level. Table only shows  
 1821 behaviors not included in the models because of low sample size.

ModeratorLevel	Boldness		Exploratory	
	Studies	Entries	Studies	Entries
Experimental	12	22	15	20
Observational	4	4	1	2

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1832 **Hierarchical model with level of behavioral measurement as moderator**

1833 **Aggressiveness**

1834 **Table 21** Statistics obtained for aggressiveness from the posterior distribution of the summary effect size in a  
 1835 hierarchical model with effect sizes nested within studies and behavioral measurement level as moderator. SD is the  
 1836 standard deviation and 95% CI are the 95% credible intervals. Prob > 0 is the probability that a behavioral trait had an  
 1837 effect size value higher than zero over all MCMC iterations. N relates to the number of studies or entries.

Aggressiveness	Mean	SD	95% CI	Prob > 0	N (Studies / Entries)
Interspecific	2.0900	1.1399	[-0.2694 , 4.2850]	0.9614	4 / 5
Intraspecific	-0.5943	0.6273	[-1.8760 , 0.6448]	0.1535	15 / 20

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**Figure 11** Posterior Distributions for aggressiveness with behavioral measurement level as moderator

1848 **Table 22** Table showing the number of studies and entries per behavioral trait and behavioral measurement level. Table  
 1849 only shows behaviors not included in the model because of low sample size.

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ModeratorLevel	Activity		Boldness		Exploratory	
	Studies	Entries	Studies	Entries	Studies	Entries
Interspecific	1	1	1	1	0	0
Intraspecific	13	20	15	25	16	22

1855 **Sample sizes for trait correlations moderators**

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1857 **Table 22** Table showing the sample size of each correlation moderator for all behavioral traits. Correlations are between  
 1858 a behavioral traits or between a behavioral trait and body mass

Correlations	Activity		Aggressiveness		Boldness		Exploratory		Sociability		Body Mass	
Behavioral Trait	Stud	Entr	Stud	Entr	Stud	Entr	Stud	Entr	Stud	Entr	Stud	Entr
Activity	-	-	3	3	3	3	0	0	1	1	1	1
Aggressiveness	3	4	-	-	2	2	0	0	0	0	3	3
Boldness	3	3	2	2	-	-	2	3	1	1	1	1
Exploratory	0	0	0	0	2	3	-	-	0	0	2	2
Sociability	1	1	0	0	1	1	0	0	-	-	0	0

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1872 **APPENDIX F. Publication Bias**

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1874 **Table 1** Results for Egger’s regression using standard error of effect sizes as a moderator in the hierarchical model with  
 1875 effect sizes nested within studies. Table shows for each behavioral trait the results obtained for the intercept and slope  
 1876 of the regression. Mean is above, and below are 95% CI.

Behavioral Trait	Activity	Aggressiveness	Boldness	Exploratory	Sociability
<b>Intercept</b>	-0.8077 [-1.9468 , 0.2646]	1.7385 [-0.5059 , 3.9763]	0.5442 [-0.3765 , 1.4905]	0.4295 [-0.3768 , 1.2635]	-0.3852 [-10.1554 , 9.3105]
<b>Slope</b>	2.7781 [0.5151 , 5.1895]	-3.3652 [-6.6872 , -0.1407]	-0.5208 [-3.5611 , 2.4392]	0.4363 [-1.7855 , 2.5824]	2.4563 [-26.4217 , 31.9472]

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