

1 **Novel mating behaviours in the squaretail grouper:** 2 **Response to “*Fake spawns and floating particles*”**

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18 **Abstract**

19 Based on two years of in-water observations of a high-density spawning aggregation of the
20 squaretail grouper in the Lakshadweep Archipelago, we described a previously unreported
21 inverse size assortment with large males courting several small females that shoaled mid-water
22 (DOI 10.1186/s12898-017-0120-5). Critiquing our manuscript, Erisman and colleagues (DOI
23 10.1186/s12898-018-0206-8) suggest that our observations and interpretation are flawed, and do
24 not fit within currently accepted theory. Here we offer a detailed counter of their main
25 methodological and theoretical criticisms. Their criticism that this reproductive tactic has never
26 been observed before is hardly a criticism since its novelty is precisely what we wished to
27 highlight. The supplementary video that Erisman et al use to base much of their criticisms was
28 not the basis of our conclusions, which relied on direct in-water observations. These observations
29 were conducted over two spawning years, taking care to ensure that we sampled aggregations at
30 peak densities. Like other researchers working on this species, we did not directly observe
31 mating, but have used courtship as a proxy for mating success – a well-established proxy across
32 mating systems studies. Apart from these methodological concerns, the authors suggest that there
33 is no theoretical support for our observations. However, sexual selection theory provides a well-
34 established framework showing that, at very high mating densities, a variety of tactics can
35 emerge, that often vary considerably between populations and locations. We agree with the
36 authors that novel observations should be scrutinised carefully. They challenge our current
37 understanding of the range of behaviours populations display and serve as a springboard for
38 theoretical advancement. We stand by our observations and hope they serve as a useful addition
39 to the fascinating and complex natural history of species like the squaretail grouper.

40

41 **Introduction**

42 In a manuscript published in the journal *BMC Ecology* (Karkarey et al 2017) we reported a rare
43 set of observations of mating behaviours of the squaretail grouper (*Plectropomus areolatus*) at a
44 spawning aggregation in the Lakshadweep Archipelago before the population was fished. The
45 densities of groupers we recorded at the aggregation were among the highest recorded anywhere,
46 and our detailed observations over two years confirmed that, at these high densities, this species
47 shows two distinct courtship tactics – a pair courtship (also recorded elsewhere across the range
48 of this species) and a previously unreported school courtship tactic. Based on in-water
49 observations we proposed that the school courtship likely leads to a unique ‘school spawning
50 tactic’ where larger males spawn with several smaller females in mid-water schools. Our
51 findings contributed to efforts by the local community and government agencies to protect the
52 aggregation from fishing – a protection that continues to this day. In a recent critique of our
53 paper, Erisman et al [2] suggest that our reported results were based on a single “fake”
54 observation of single-male multi-female spawn without empirical or theoretical basis, that we
55 likely did not observe actual spawning, and that the inverse-size assortment we report is based on
56 invalid methods and an inaccurate interpretation of theory. These allegations are troubling since
57 we have clearly set out the theoretical framework of sexual selection and mating systems in our
58 paper, used standard ecological and behavioural methodologies, and carefully discussed our
59 inferences together with the limitations of our study and future directions to test the explanations
60 we propose. We encourage readers to read through these in detail in our original manuscript,
61 Karkarey et al [3].

62

63 Our paper documented mating behaviours of the squaretail grouper at a natural and extreme end
64 of the density spectrum that had not been previously addressed in the literature. The squaretail
65 grouper has more usually been observed at spawning aggregations exposed to years of fishing
66 and human disturbance. We monitored reproductive behaviour for over two years in the absence
67 of fishing activities, using carefully designed and well-established ecological and behavioural
68 methodologies. At peak densities, we recorded an average of 72.08 ± 27.46 fish per 1000 m³
69 (200m² x 5m depth) across the spawning site. Densities were more than 4 times higher where we
70 documented the alternative school spawning tactic [3]. Our paper explores how these
71 observations might add to our understanding of the maintenance of alternative reproductive
72 tactics. Our paper lays out the limitations of this observational study and makes clear that it is not
73 a confirmatory test of hypotheses for the evolution of the alternative reproductive behaviours we
74 report. Rather, we use the broader theory of sexual selection together with detailed behavioural
75 data to propose plausible evolutionary explanations for the interesting behavioural variation we
76 report. The two main processes we draw upon are:

77

- 78 1. the influence of density on the expression of alternative reproductive tactics and
- 79 2. the role of female behaviour and choice in influencing male mating tactics.

80 Both these are common processes that have been tested across the animal kingdom.

81
82 Here, we respond to the allegations made by Erisman et al [2], describing in detail why we think
83 our methodology, inferences and explanations are robust and contextually relevant to studying
84 natural history and animal behaviour. Their principal concerns with our study are broadly
85 methodological (false observation of spawning event, not sampling at peak spawning periods,
86 and using invalid measures of courtship rates) and theoretical (no support for single male-multi
87 female mating in broadcast spawning fish). We address each of these points in the sequence in
88 which they raise them.

89

90 **Detailed Responses**

91 **Issue 1: False observations of spawning events involving a single male with multiple** 92 **females**

93

94 The authors base much of their critique on a forensic analysis of the supplementary video we
95 submitted along with the manuscript, using it to reject our observations of the spawning events.
96 However, they give the video more importance than it deserves. At no point in our paper do we
97 present the video as conclusive evidence but merely as supporting what we observed in situ. The
98 video was captured by a remote underwater camera, when we were NOT in the water. The
99 lengthy discussion they devote to the ‘sperm cloud’ being a floating piece of faeces is entirely
100 irrelevant as we never make claim to the contrary. The two incidents of ‘school spawning’ have
101 been described as a sequence of events , culminating in gamete release in our manuscript [3].
102 These were observed directly by us in the water, at a distance of less than 5m from the female
103 school. These observations of natural history have been recorded in the text of our original paper
104 in as clear and precise a way as possible ([3], pages 5 & 6). The video merely adds to our
105 confidence of the prevalence of ‘school courtship’ and potential spawning behaviour. The work
106 of Johannes [4, 5], Johannes et al. [6] and Pet et al. [7], which Erisman et al [2]. have
107 mentioned, have documented reproductive behaviours in groupers in much the same way, i.e.
108 relying on direct in-water observations or on many of the same proxies that we have used (ie.
109 swollen bellies, spawning colouration, male behaviours, etc). As we explain in the paper,
110 because the aggregation was seasonally protected, more invasive and destructive techniques were
111 not available to us. More generally, in diverse taxa, behavioural work is commonly conducted
112 using direct observations, especially for rare behaviours (see for instance, 8-10). It is therefore
113 puzzling that the authors have taken the video as our primary (or only) evidence, when the
114 original article makes it clear that it is the direct observations that are the primary evidence (a
115 mis-reading of our words that is repeated time and again throughout their commentary).

116

117 **(2) No empirical evidence of single male - multiple female spawning in *P. areolatus*,**
118 **groupers, or any other coral reef fish**

119

120 Erisman et al [2] provide descriptions of the behaviour of female shoals and squaretail groupers
121 as observed in other regions and critique the behavioural observations in our paper based on
122 them not having been reported earlier. It is difficult to know how to respond to this critique,
123 given that the precise purpose of our manuscript was to report observations we believed were
124 unique and noteworthy. While these behaviours were certainly brief and anomalous to what is
125 known, we emphasize that they were observed multiple times across two years, under specific
126 density conditions in this population.

127
128 Even while doubting our observations of unique mating behaviour, Erisman et al. [2] insist that
129 there is nothing unique about ARTs in the *P. areolatus*. They provide a detailed account of other
130 ARTs reported for this species by past researchers [4-7,11] from different regions. We agree with
131 the authors that the schooling behaviour of female squaretail grouper schools is not novel and
132 has been reported previously [6]. We acknowledge this in our paper, but emphasize the
133 differences as we observed them in the Lakshadweep aggregation. In particular, we describe that
134 female shoals were larger than reported previously (>150 females), size-specific, and unlike the
135 descriptions provided by Johannes et al [6], the schools formed a cohesive unit – ie. females did
136 not break free from this school to follow males into their territories after male courtship forays
137 ([3], page 5). The Palauan multiple male-single female courtship interaction that Johannes et al
138 [6] recorded had a very high male:female ratio unlike the Bitra aggregation. In the same paper,
139 Johannes et al [6] also describe that “*In a Solomon Islands spawning aggregation, where female*
140 *P. areolatus outnumbered males, Johannes [1989] observed that the males were typically*
141 *attended by several females, and he saw no harassment of females by males*”. This description
142 resembles our observations of single male – multiple female associations on the slope, where
143 population sex ratios were highly skewed towards females. Together, these observations only
144 strengthen the growing understanding that, at high densities, species may employ a wide suite of
145 reproductive tactics that are lost as densities decline. There exists a substantial behavioural
146 ecology literature showing that mating tactics can vary between closely related species, between
147 populations of the same species, and even within a population [12-16]. A wide variety of factors,
148 including population density, operational sex ratios, habitat, and environmental contexts can lead
149 to differential expression of mating and other behaviours [12,15,19]. For example, the lek-mating
150 system is seen in fewer than 0.5% of birds and 0.2% of mammals [18]. Several lekking ungulates
151 show cross-population variation in mating behaviour, with only a few populations showing
152 lekking [12,19]. Furthermore, lekking may disappear from a population when density declines,
153 for example due to hunting [12].

154
155 The authors of the critique call into question our observations and our broader understanding of
156 grouper mating systems, although we have specifically acknowledged the diversity of mating
157 strategies of groupers with relevant citations ([3] Page 2). As we clearly explain in our paper, the
158 behaviour we report may be associated with particularly high density aggregations, which as we
159 report, is extremely rare given the strong fishing pressures experienced by these groupers

160 globally [20]. It is therefore not surprising that such behaviours have not been observed
161 previously (including by Erisman et al). All the more reason, then, to carefully report these
162 behaviours when they are observed, since they greatly inform our understanding of high-density
163 mating tactics.

164

165 **(3) No theoretical support for single male - multiple female spawning in broadcast** 166 **spawning fishes**

167

168 A major point of contention is how population density specifically affects grouper mating
169 systems. Erisman et al state that mate monopolization by territorial males is negatively correlated
170 with population density in groupers, supported by empirical evidence and their own review [21].
171 They expect that at lower densities, pair spawning and territorial tactics exist and with increasing
172 density, group spawning is seen. We have no argument with this at the usual density ranges
173 earlier reported for this species. However, as we are at pains to report in our manuscript, at
174 densities much higher than previously reported, other tactics might arise, when both mate
175 competition and mating stakes are high enough to select for an alternative (and more costly) way
176 of gaining mates. The tactics we identify are the conventional pair spawning one (which, in our
177 system, appears to be a low-cost, low-benefit tactic) and the high-cost, high-benefit tactic of
178 ‘school spawning’. We describe this in elaborate detail in our paper [3]. In this tactic, large males
179 hold territories in a dense aggregation that provide access to large female schools. But courtship
180 and mating takes place external to these territories. Males temporarily leave these territories to
181 make forays into the schools, which is highly costly, as males risk losing their territories, but at
182 the same time, may benefit from gaining seven times higher potential mating opportunities.
183 Thus, like Erisman et al, we also argue that at high densities, conventional mate monopolisation
184 through pair spawning is increasingly difficult. The sole point of contention appears to be that
185 Erisman et al [2] expect only group spawning under high density while we report a different
186 school spawning tactic, that we suggest may be a variation of, or precursor to, group spawning
187 ([3] page 9).

188

189 Variation in mating tactics between populations of the same species is hardly unusual. Density
190 (or potential mates) can interact with environmental factors to affect mating tactics in complex
191 ways [22]. We would once again like to reiterate that the densities we reported in this
192 aggregation are higher than those reported previously in squaretail grouper aggregations, so it is
193 not surprising that the behaviour we report has not been previously discussed – and precisely
194 why we believed it was important to report. Refuting a tactic we report based on that it has not
195 been reported before is not a valid criticism.

196

197 Erisman et al [2] state that we report puzzling female behaviours without placing them in the
198 context of theory. Particularly they ask “*Why would multiple females choose to risk their eggs on*
199 *a single male’s sperm release when numerous other males are present?*”, *alleging that we claim*

200 “egg competition”. This bears some explanation.

201
202 Firstly, there is a rich body of work showing that male and female mating tactics are more
203 variable than previous thought. Males and females may make mating decisions that are not
204 initially “intuitive” but are adaptive when studied over individual lifetimes. For example,
205 paternity studies have shown that in bighorn sheep (*Ovis canadensis*), subordinate, younger
206 males following a ‘low-benefit’ harassment tactic gain almost as much paternity as dominant
207 males following a mate-guarding tactic [25]. Similarly, in many taxa, females engage in covert
208 matings with subordinate, younger or satellite (often presumed to be of lower quality) males
209 (e.g., 26, 27).

210
211 Secondly, multiple females mating with a single male is not puzzling but seen commonly as in
212 the case of leks. In lek mating systems, females are commonly choosy about mates, exhibit
213 strong mate choice and mating success is commonly highly skewed towards a small percentage
214 of males. In addition, even in such extreme polygynous systems, associations between multiple
215 females and a single male, and female-female competition for individual males on leks have
216 been reported [28]. Depending on male quality or site quality or direct benefits gained from
217 males, females may show unanimous mate choice which may result in multiple females
218 associating with the same individual males. At no point do we claim ‘egg competition’ but we
219 assume the authors of the critique refer to the situation of multiple females associating with a
220 single male in a short period of time - discussed in the literature in the context of sperm
221 limitation. In our paper we propose that females show condition dependence, with smaller
222 females potentially trading off current reproductive success with growth for potentially higher
223 reproductive success in the future. In the literature, this trade-off between growth and current
224 reproductive success is seen when females run the risk of sperm limitation [29]. These provide
225 plausible explanations for the question posed by the critics: why females would “*choose to risk*
226 *their eggs on a single male’s sperm release when numerous other males are present*”. We have
227 acknowledged in our manuscript that these explanations remain to be tested by other, more direct
228 methodologies in this aggregation.

229
230 The possibilities described above are discussed at length in our paper, and we are puzzled that
231 the authors appear to have missed them while claiming that we do not provide plausible
232 explanations from within the classical and current theory of sexual selection, life history theory
233 and ARTs. However, even had we not been able to think of plausible explanations from current
234 theory for our observations, it would not be a reason to not report them.

235 236 **(4) Insufficient evidence that observations were made during the actual spawning period**

237
238 The authors suggest that we did not sample during spawning periods. However, as we described
239 in detail in the paper ([3] page 3), we carefully established spawning seasonality and diel

240 specificity of this aggregation by conducting extensive in-water surveys across months and lunar
241 phases. We supplemented our direct inwater surveys with the help of local informants who
242 monitored the site in our absence.

243
244 To reiterate, we found that groupers arrive two days before the new moon, reached their highest
245 densities on new moon day and then dropped in density by 80% the day after new moon, and by
246 98% by the third day after the new moon. In the absence of histological means to assess
247 spawning time, we triangulated the spawning time based on the dramatic drop in densities after
248 new moon day and the absence of highly gravid females at the aggregation site after new moon
249 days. In addition to this, from our focal behavioural observations we found that males spent upto
250 50% more time in intra-sexual aggression on the evenings of new moon days compared to days
251 and periods prior to and after the new moon. Taken together, our in-water observations gave us
252 enough confidence that we were sampling as close to the spawning period as possible (ie.
253 afternoons of new moon days).

254 255 **(5) No evidence of “inverse size-assortment” due to invalid methods used to estimate** 256 **courtship rates**

257
258 The criticism that we used invalid methods to estimate courtship rates has also been carefully
259 addressed in our paper. We have clearly described that we do not measure courtship rates, but in
260 fact measure ‘association rates’ as a proxy for ‘potential mating opportunities’ ([3], page 4).
261 However, considering that this is a fish spawning aggregation, and that sampling was conducted
262 close to spawning period (on peak aggregation days), it is reasonable to assume that male-female
263 interactions were courtship, especially when the sequence of behaviours that we observed and
264 describe in the paper has been documented as courtship behaviours in other studies of this
265 species [4].

266
267 Male fitness is ideally measured over an individual’s life time and using genetic methods to
268 determine paternity [30]. However, such assessments of male fitness are rare for wild
269 populations. Studies of diverse taxa and both in the field and in the lab typically use proxies of
270 fitness, e.g., number of offspring, number of matings, number of females a male associates with
271 [31-34]. The last measure, the number of females a male associates with, is a commonly used
272 proxy for male reproductive success in wild populations [31-33,35,36]. Even in controlled
273 experiments in the lab, associations between males and females are taken to represent mating
274 decisions - for example, experiments on female preference for male phenotype in many taxa use
275 the time spent by a female close to a male (or model) as indicative of her preference of mate [37-
276 39].

277
278 We have clearly stated in our paper [3] that we use association rates as a proxy for potential
279 mating opportunities. We explain why mating rates are a challenge to measure (like in many

280 other taxa) and also explain why we believe our index serves as a reasonable proxy for potential
281 mating opportunities.

282

283 **Conclusions**

284 We wholeheartedly agree with Erisman et al of the need for rigour and care in understanding
285 mating behaviour. Our interpretation of the ecology of mating systems and the arguments we
286 make are actually very similar to the ones Erisman et al [2] have themselves laid out in their
287 criticism. Our suggestion that high density can favour the appearance and maintenance of
288 alternative reproductive tactics is supported by theory [22] and empirical work [22, 23]. .
289 Furthermore, the argument we make that differences in female spatial distribution and
290 preferences can maintain multiple male mating tactics is also supported in the literature [40, 41].

291

292 The broad arguments made by us and Erisman et al (that male and female mating tactics may be
293 density dependent) actually match, differing largely in the specifics of the behaviour displayed
294 under high density that we report versus that expected by the critics. Most of the criticisms
295 appear to stem from the authors misreading our original paper. We would encourage the authors
296 and all readers to once again closely read our methodology to resolve any remaining confusion.
297 We thank the authors for their patient criticisms and we encourage them in turn to engage with
298 the wider theory of mate choice and sexual selection with open mindedness. Writing in the
299 1970s, Paul Feyerabend was convinced that unsavoury brawling was unavoidable in science, but
300 he was even more insistent that a proliferation of observations and theories is required to
301 overcome the ‘chauvinism of science that resists alternatives to the status quo’ [1]. As our
302 observations show, species like the squaretail grouper have a broader suite of reproductive tactics
303 than previously imagined. It does not challenge what we know about the species, it instead adds
304 to it.

305

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309

310 **References**

311

- 312 1. Feyerabend, Paul. 1975. *Against Method*. New Left Books. London.
- 313
- 314 2. Erisman BE, Barreiros JP, Rhodes K and Warner R. 2018. Fake spawns and floating
315 particles: a rebuttal of Karkarey et al. “Alternative reproductive tactics and inverse size-
316 assortment in a high-density fish spawning aggregation”. *BMC Ecol*. Doi ;
317 10.1186/s12898-018-0206-8.

318

- 319 3. Karkarey R, Zambre A, Isvaran K, Arthur R. Alternative reproductive tactics and inverse
320 size-assortment in a high-density fish spawning aggregation. *BMC Ecol.* 2017;17(1):10.
321
- 322 4. Johannes RE. Reproductive strategies of coastal marine fishes in the tropics. *Environ Biol*
323 *Fishes.* 1978; 3:65–84.
324
- 325 5. Johannes RE. Spawning aggregation of the grouper, *Plectropomus areolatus* (Ruppel) in
326 the Solomon Islands. Proceedings of the 6th International Coral Reef Symposium:
327 Australia, Vol 2. 1988. p.751–55.
328
- 329 6. Johannes RE, Squire L, Graham T, Sadovy Y, Renguul H. Spawning aggregations of
330 groupers (Serranidae) in Palau. Arlington: Marine Conservation Research Series Publ.
331 #1, The Nature Conservancy; 1999.
332
- 333 7. Pet JS, Mous PJ, Muljadi AH, Sadovy YJ, Squire L. Aggregations of *Plectropomus*
334 *areolatus* and *Epinephelus fuscoguttatus* (groupers, Serranidae) in the Komodo National
335 Park, Indonesia: monitoring and implications for management. *Environ Biol Fishes.*
336 2005;74:209-18.
337
- 338 8. Bro-Jørgensen J. Overt female mate competition and preference for central males in a
339 lekking antelope. *Proc Nat Acad of Sci.* 2002; 99(14): 9290-9293.
340
- 341 9. Young, K.A., Genner, M.J., Joyce, D.A. and Haesler, M.P. Hotshots, hot spots, and
342 female preference: exploring lek formation models with a bower-building cichlid fish.
343 *Behav Ecol.* 2009; 20(3): 609-615.
344
- 345 10. Surbeck M, Mundry R, Hohmann G. Mothers matter! Maternal support, dominance status
346 and mating success in male bonobos (*Pan paniscus*). *Proc R Soc Lond B Biol Sci.*
347 2011; 278(1705): 590-598.
348
- 349 11. Rhodes KL, Nemeth RS, Kadison E, Joseph E. Spatial, temporal, and environmental
350 dynamics of a multi-species epinephelid spawning aggregation in Pohnpei, Micronesia.
351 *Coral Reefs.* 2014;33:765–75.
352
- 353 12. Clutton-Brock, T. H., & Vincent, A. C. Sexual selection and the potential reproductive
354 rates of males and females. 1991; *Nature*, 351(6321), 58.
355
- 356 13. Lott, D. F.. Intraspecific variation in the social systems of wild vertebrates (Vol. 2). 1991;
357 Cambridge University Press.
358

- 359 14. Apollonio, M. Lekking in fallow deer: just a matter of density?. *Ethol Ecol Evol.*
360 1989; 1(3): 291-294.
361
- 362 15. Brockmann HJ. The evolution of alternative strategies and tactics. *Adv Study Behav.*
363 2001; 30: 1-51.
364
- 365 16. Taborsky M. Alternative reproductive tactics in fish. In: Oliveira RF, Taborsky M,
366 Brockmann HJ, editors. *Alternative reproductive tactics: an integrative approach.* New
367 York: Cambridge University Press; 2008. p. 263–311.
368
- 369 17. Tomkins, J. L., & Brown, G. S. Population density drives the local evolution of a
370 threshold dimorphism. *Nature.* 2004; 431(7012): 1099.
371
- 372 18. Davies NB. Mating systems. In: Krebs JR, Davies NB (eds). *Behavioural ecology*, 3rd
373 edn. 1991; Blackwell, Oxford.
374
- 375 19. Thirgood, S., Langbein, J., and Putman, R., J. Intraspecific variation in ungulate mating
376 strategies: the case of the flexible fallow deer. *Adv Study Behav.* 1991; 28: 333.
377
- 378 20. Sadovy de Mitcheson YS, Craig MT, Bertoni AA, et al. Fishing groupers towards
379 extinction: a global assessment of threats and extinction risks in a billion dollar fishery.
380 *Fish Fish.* 2013;14:119–36.
381
- 382 21. Erisman BE, Craig MT, Hastings PA. A phylogenetic test of the size-advantage model:
383 Evolutionary changes in mating behavior influence the loss of sex change in a fish
384 lineage. *Am Nat.* 2009;174:83-99.
385
- 386 22. Kokko H, Rankin DJ. Lonely hearts or sex in the city? Density-dependent effects in
387 mating systems. *Philos Trans R Soc Lond B Biol Sci.* 2006;361:319–34.
388
- 389 23. Clutton-Brock TH, Rose KE, Guinness FE. (1997). Density-related changes in sexual
390 selection in red deer. *Proc Nat Acad of Sci.* 264; 1387:1509-1516.
391
- 392 24. Bonenfant C, Gaillard JM, Loison A, Klein F. Sex-ratio variation and reproductive costs
393 in relation to density in a forest-dwelling population of red deer (*Cervus elaphus*). *Behav*
394 *Ecol.* 2003; 14: 862–869.
395
- 396 25. Hogg JT, & Forbes SH. Mating in bighorn sheep: frequent male reproduction via a high-
397 risk “unconventional” tactic. *Behav Ecol Sociobiol.* 1997; 41(1): 33-48.
398

- 399 26. Lank DB, Smith CM, Hanotte O, Ohtonen A, Bailey S, Burke T. High frequency of
400 polyandry in a lek mating system. *Behav Ecol*. 2002; 13(2): 209-215.
401
- 402 27. Ortega J, Maldonado JE, Wilkinson GS, Arita HT, Fleischer RC. Male dominance,
403 paternity, and relatedness in the Jamaican fruit-eating bat (*Artibeus jamaicensis*). *Mol*
404 *Ecol*. 2003; 12: 2409-2415.
405
- 406 28. Bro-Jørgensen J. The significance of hotspots to lekking topi antelopes (*Damaliscus*
407 *lunatus*). *Behav Ecol Sociobiol*. 2003; 53(5): 324-331.
408
- 409 29. Berglund A. Egg competition in a sex-role reversed pipefish: subdominant females trade
410 reproduction for growth. *Evolution*. 1991; 45(3): 770-774.
411
- 412 30. Clutton-Brock T, & Sheldon BC. Individuals and populations: the role of long-term,
413 individual-based studies of animals in ecology and evolutionary biology. *Trends Ecol*
414 *Evol*, 2010; 25(10): 562-573.
415
- 416 31. Alberts SC, Watts HE, & Altmann J. Queuing and queue-jumping: long-term patterns of
417 reproductive skew in male savannah baboons, *Papio cynocephalus*. *Anim Behav*. 2003;
418 65(4): 821-840.
419
- 420 32. Alonso JC, Magaña M, Palacín C, & Martín CA. Correlates of male mating success in
421 great bustard leks: the effects of age, weight, and display effort. *Behav Ecol Sociobiol*.
422 2010; 64(10): 1589-1600.
423
- 424 33. Jiguet F, & Bretagnolle V. Sexy males and choosy females on exploded leks: correlates
425 of male attractiveness in the Little Bustard. *Behav Processes*. 2014; 103: 246-255.
426
- 427 34. Brommer JE, Ahola K, & Karstinen T. The colour of fitness: plumage coloration and
428 lifetime reproductive success in the tawny owl. *Proc R Soc Lond B Biol Sci*. 2005;
429 272(1566): 935-940.
430
- 431 35. Lappin AK, & Husak JF. Weapon performance, not size, determines mating success and
432 potential reproductive output in the collared lizard (*Crotaphytus collaris*). *Am Nat*. 2005;
433 166(3): 426-436.
434
- 435 36. Jiguet F, & Bretagnolle V. Manipulating lek size and composition using decoys: an
436 experimental investigation of lek evolution models. *Am Nat*. 2006; 168(6): 758-768.
437

- 438 37. Godin JGJ, Herdman EJ, & Dugatkin LA. Social influences on female mate choice in the
439 guppy, *Poecilia reticulata*: generalized and repeatable trait-copying behaviour. Anim
440 Behav. 2005; 69(4): 999-1005.
441
- 442 38. Griggio M, Biard C, Penn DJ, & Hoi H. Female house sparrows “count on” male genes:
443 experimental evidence for MHC-dependent mate preference in birds. BMC Evol Biol.
444 2011; 11(1): 44.
445
- 446 39. Heuschele J, Mannerla M, Gienapp P, & Candolin U. Environment-dependent use of
447 mate choice cues in sticklebacks. Behav Ecol. 2009; 20(6): 1223-1227.
448
- 449 40. Clutton-Brock T. Sexual selection in males and females. Science. 2007; 318(5858): 1882-
450 1885.
451
- 452 41. Stockley P, & Bro-Jørgensen J. Female competition and its evolutionary consequences in
453 mammals. Biol Rev. 2011; 86(2): 341-366.
454