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2   Female song and aggression show contrasting relationships to

3   reproductive success when habitat quality differs

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15

16 **Abstract**

17 Though well studied in males, little is known about the factors influencing variation

18 in expression of exaggerated traits such as intense aggression, elaborate ornaments,

19 and lethal weaponry in females. Current research suggests that these traits are

20 important when females compete for access to limited reproductive resources, and

21 that greater trait expression leads to higher reproductive success. However, contest

22 theory predicts that differences in resource availability will alter the costs and

23 benefits of competition and contest rules, potentially changing the strength or

24 direction of selection. Female superb fairy-wrens, a common Australian passerine,

25 compete for exclusive breeding territories using song and aggression. A previous

26 study in a population residing in uniform, high-quality habitat found that strong

27 responses to a simulated intruder were associated with improved reproductive

28 success. Here, we determine whether differences in resource availability, i.e. habitat

29 quality, are associated with changes to this relationship by replicating this study in a

30 second population that resides in lower quality, patchy habitat. We quantified

31 female response (activity and song rates) to a simulated same-sex intruder, and

32 examine the relationships with territory quality and annual reproductive success.

33 Contrary to previous research, we found that in low quality, patchy habitat, stronger

34 responders occupied poorer quality territories and had lower reproductive success.

35 However, basal song rates and responses to an intruder were overall much stronger

36 in low quality habitat. These results suggest that female-female contest rules and

37 the intensity of competition differ according to resource availability, which may

38 alter how selection acts on female competitive traits.

39

40   **Key words:** aggression, competitive traits, contests, female competition, female

41   song, population differences

42

43   **Significance statement:**

44   Females appear to use costly social traits, e.g. ornaments, armaments, complex song

45   and aggression, in the context of female-female competition for limited resources.

46   However, very little is known about how changes in resource availability might alter

47   female-female contest rules or the relationship between trait expression and fitness

48   estimates. Previous research in a population of superb fairy-wren, a songbird,

49   residing in high quality habitat, found that female song and aggression were

50   positively related to reproductive success. Here, we replicate that study in a

51   population that resides in low-quality, patchy habitat. We found higher levels of

52   aggression and song, and that the relationship between behavior and fitness was in

53   the opposite direction. This suggests that resource availability can affect female

54   behavior, dramatically alter the strength and direction of selection, and may change

55   the rules females observe when engaging in contests.

56

57   **INTRODUCTION**

58   Females in a variety of taxa and mating systems express traits similar to those used

59   by males when competing for access to females, i.e. competitive traits such as

60   aggression, ornaments, weaponry, etc. (West-Eberhard 1983; Cain and Ketterson

61   2012; Tobias et al. 2012; Cain and Rosvall 2014). Though females are generally not

62   mate-limited, they are often limited by their ability to access other reproductive

63   resources such as high quality males, parental assistance, oviposition sites,

64   dominance rank, and territories (West-Eberhard 1983; Clutton-Brock 2009). If

65   variation in female ability to acquire and defend these resources leads to differential

66   reproductive success, then selection may favor the expression of competitive traits

67   in females, regardless of whether the resource is mates or some other reproductive

68   resource (Crook 1972; West-Eberhard 1983; Tibbetts 2008; Elias et al. 2010;

69   Rosvall 2011a; Tobias et al. 2012). Because this form of selection acts via social

70   competition, but not necessarily via competition for mate number or mate quality, it

71   has been termed social selection; sexual selection is considered a special case of

72   social selection (West-Eberhard 1983).

73

74   Social selection predicts that more competitive females will have better access to

75   limited resources and that competitive trait expression should be higher or more

76   beneficial when critical resources are more limited (West-Eberhard 1983; Clutton-

77   Brock 2009; Elias et al. 2010; Rosvall 2011a; Stockley and Bro-Jørgensen 2011;

78   Tobias et al. 2012). Empirical work supports this possibility; increased levels of trait

79   expression are associated with improved access to limited resources, and trait

80   expression is positively related to reproductive success in a variety of species (Elias

81   et al. 2010; Rosvall 2011a; Stockley and Bro-Jørgensen 2011; Cain and Ketterson

82   2012; Tobias et al. 2012; Cain and Ketterson 2013; Cain and Rosvall 2014; Cain et al.

83   2015; Brunton et al. 2016). However, the rules animals observe when engaged in

84   contests over resources can change according to the value, availability, and

85   distribution of the resource, as well as the density of competitors (Grafen 1987;

86   Grant and Guha 1993; Lindström and Pampoulie 2004; Noël et al. 2005). The

87   intensity of resource defense is predicted to change according to the economic

88   defendability of the resource (benefits – costs), increasing as the resource becomes

89   more limited or clumped, and decreasing when the resource is more evenly

90   distributed or the number of competitors is too high (Emlen and Oring 1977; Grant

91   1993; Grant and Guha 1993; Noël et al. 2005). Further, when the consequences of

92   failure are extreme, i.e. death or no reproductive success, the costs of fighting are

93   less than the costs of losing, creating a divisive asymmetry (Grafen 1987). When

94   such asymmetries occur, individuals unlikely to win future contests are predicted to

95   respond intensely to any threat (Grafen 1987). As a consequence, changes in

96   resource availability may alter female contest rules and the relationship between

97   female competitive trait expression and fitness. However, such relationships have

98   rarely been directly examined. The few studies that have directly examined the role

99   of resource value in the context of female-female competition report that contest

100   rules are often quite different from what is observed in males (Draud 2004; Tibbetts

101   2008; Elias et al. 2010).

102

103   Superb fairy-wrens (*Malurus cyaneus*) are an excellent model for exploring the

104   relationships between resource availability, competitive trait expression, and fitness

105   in females. Superb fairy-wrens are socially monogamous and cooperative breeders;

106   roughly half of the breeding pairs have subordinate males, often sons from previous

107   broods, assisting in nest defense and offspring provisioning (Rowley and Russell

108   1997; Cockburn et al. 2003). In contrast, daughters disperse and must acquire a

109   territory of their own. Territories are critical for survival and reproductive success,

110   and there are no floater females (Cooney and Cockburn 1995). Superb fairy-wrens

111   also reside in a range of habitats (Rowley and Russell 1997), permitting exploration

112 of relationships in habitats of varying quality. Female superb fairy-wrens use song

113 and aggression to compete with one another for access to limited territories

114 (Cooney and Cockburn 1995; Cain and Langmore 2015). In a recent study on

115 females residing in high quality and relatively uniform habitat, female response to a

116 simulated competitor was positively associated with annual reproductive success

117 (Cain et al. 2015). However, because differences in resource availability can alter the

118 costs and benefits of defense (Emlen and Oring 1977; Grant 1993; Cain and Rosvall

119 2014), and change the consequences of losing contests (Grafen 1987; Tibbetts 2008;

120 Elias et al. 2010), different populations may experience different selective optima

121 for trait expression.

122

123 Here we examine how differences in resource availability might alter the functional

124 consequences of female trait expression by examining the relationships between

125 trait expression, resource acquisition, and annual reproductive success, in a

126 separate population of superb fairy-wrens inhabiting lower quality habitat with

127 higher variability in territory quality than in our previous study. Resource defense

128 theory predicts that the higher variability of territory quality and the reduced

129 number of competitors would increase the benefits of aggression (Grant 1993;

130 Grant and Guha 1993; Noël et al. 2005), predicting that overall aggression may be

131 higher in the focal population than in the previous study, where territory quality is

132 less variable and population density is higher. Social selection theory predicts that if

133 aggression and song rates signal competitive ability, more responsive females will

134 inhabit better quality territories and have higher reproductive success.

135 Alternatively, contest theory predicts that because the costs of losing to an intruder

6

136   are very high, females that are unlikely to acquire another territory, i.e. those on low

137   quality territories, will act as desperados and escalate despite the potential costs. If

138   so, female response is predicted to be negatively related to territory quality and

139   breeding success.

140

141   **METHODS**

142   **Study species, populations and territory quality**

143   The superb fairy-wren is a common, socially monogamous, cooperatively breeding

144   Australian songbird. Because territories are essential for survival and reproductive

145   success, females often compete vigorously to acquire territories and defend

146   ownership (Cooney and Cockburn 1995). Females re-nest after nest failure or after

147   fledglings reach independence if conditions remain suitable for breeding, and may

148   produce as many as three successful broods of young in a single season. Territorial

149   behavior begins in August (Cockburn et al. 2009), though first eggs are generally

150   laid mid-October (Dunn and Cockburn 1996). Young females disperse at the end of

151   the breeding season, or just before the start of the next season, after which they are

152   highly philopatric (Cockburn et al. 2003). Previous work reported that roughly 60%

153   of females acquire a breeding position (Mulder 1995). Females that do not acquire a

154   breeding position by mid-November disappear from the population, there are no

155   floater females, and data from previous work suggests that these females die

156   (Pruett-Jones and Lewis 1990; Mulder 1995). As a consequence, the sex-ratio

157   becomes heavily male biased as reproduction begins (Cockburn et al. 2003).

158

159   The focal population resides in 130 hectares of open eucalypt woodland in Campbell

160   Park (CP), ACT, Australia (149°9′ E, 35°16′ S). This site is approximately 7km from

161   the site of our previous study in the Australian National Botanic Garden (ANBG, Cain

162   et al. 2015). Overall habitat quality in CP is relatively low; there is no artificial

163   watering, and there is limited and patchy distribution of the dense underbrush

164   important for fairy-wren nesting (Nias 1984; Rowley and Russell 1997). Population

165   densities vary annually (e.g. Langmore and Kilner 2007), and during most years

166   only a portion of the territories are occupied. Territory quality may vary depending

167   on availability of food, water, nest sites or refuges from predators. Rather than

168   making arbitrary decisions about the relative importance of these variables for

169   fairy-wrens and classifying territory quality accordingly, we instead quantified the

170   territory preferences of the birds themselves. Using records from 2003-2011 (the

171   breeding seasons prior to the study), we scored each territory for occupancy rate

172   (proportion of breeding seasons the territory was occupied). Territory boundaries

173   are consistent across season, but territories were considered occupied if a group

174   was using at least half of the historical territory. In high-density years, all 26

175   territories investigated were occupied, however in low-density years as few as 8

176   were occupied (mean = 0.54, SE = 0.06, range = 0.125 – 1.0). This contrasts with the

177   occupancy rate in our previous study in high quality, irrigated habitat, the

178   Australian Botanic Gardens (BG) (Cain et al. 2015), where all territories were

179   occupied every year of the same timespan. These apparent differences in habitat

180   quality between the two sites were also reflected in different densities of fairy-

181   wrens; during this study, SFW density in CP was 0.6 females per hectare; density in

182   BG was 1.23 females per hectare. Because superb fairy-wren are widely distributed

183   across good and poor quality habitat, and Australian weather patterns can change

184   abruptly from year to year (Mac Nally et al. 2009), we view the two populations as

185   examples of naturally occurring high and low habitat quality.

186

187   **General field methods**

188   All adults were uniquely color-banded, and breeding groups were observed on a

189   regular schedule to monitor all nesting attempts and determine group composition

190   (number of subordinates). We used previous years' banding records to determine

191   each female's age; all females were classified as group or pair breeding, and as

192   young (first year breeding) or old (after first year) accordingly. Fairy-wrens are

193   highly philopatric after their first breeding season (Mulder 1995) allowing accurate

194   aging of immigrating females. Because previous work found that length of territory

195   residency is important for female song rates (Cooney and Cockburn 1995), we also

196   categorized females as to whether they were on a new territory, relative to the

197   previous year. Across the entire breeding season we recorded the total number of

198   fledglings produced. Females that produced at least one successful nest throughout

199   the entire season (at least 1 fledgling) were classified as successful; if all attempts

200   failed before fledging, the female was classified as failed.

201

202   **Simulated territorial intrusions**

203   To simulate a foreign female intruding on the resident female's territory we used

204   the established paradigm for male territoriality research. Details are available

205   elsewhere (Cain et al. 2015). Briefly, focal territory-holding females were identified

206   (n=26) and trials were conducted opportunistically based on female breeding stage

207　(pre-breeding or nest building), between 15 September and 15 November of 2012.

208　We observed females for 10minutes and recorded song rate (songs per minute) and

209　then began the playback trial. Each focal female heard a series of foreign songs (see

210　*playback construction* below). We recorded latency to respond, song rate, time spent

211　within 5 m, and the number of flights greater than 1 m (requires actual flight rather

212　than hopping). A single observer (KEC) observed all trials and was blind to territory

213　quality and reproductive success.

214

215　To contrast the response of the two populations and avoid multiple comparisons we

216　used Principal Component Analysis to condense the observed variation in responses

217　(number of songs, flights, time spent within 5 m, and latency to respond). The first

218　PC explained 58% of the observed variance and was used for all further analysis

219　(eigenvalue = 2.3, Loadings: Latency to respond = -0.87, Flights = 0.79, Song rate =

220　0.72, time within 5 m = 0.60). A high response score indicated a stronger response

221　(i.e., a quicker response, more songs and flights, and more time near the speaker).

222

223　**Playback construction**

224　To minimize pseudoreplication we constructed 18 playback recordings of foreign

225　songs, for details of song recording and playback construction see Cain and

226　Langmore (2015). Briefly, each playback consisted of two unique female songs

227　(from the same individual), each song was played three times in two bouts (six

228　total), alternating between song one and two. There was 20 s of silence between

229　songs within a bout, and 45 s of silence between bouts. The total playback was

230　approximately 400 sec long. The song to silence ratio (1:7), and the length (370s),

231   and amplitude (85 dB sound pressure level) of the playback were consistent with

232   observed natural variation in female song (Cooney and Cockburn 1995). To avoid

233   familiarity effects (Cooney and Cockburn 1995; Brunton et al. 2008) we used only

234   foreign songs; i.e. females heard playbacks constructed from songs recorded at one

235   of three other sites, all at least 7km away, one (BG) was the site of the previous

236   study; The Australian Botanic Gardens, Coppin's Crossing and The Pinnacle Reserve.

237   Birds in the previous study heard songs from Campbell Park (this study), Coppin's

238   Crossing and The Pinnacle Reserve. The two off-site locations were not study

239   populations so little information is available regarding habitat quality. However,

240   neither was irrigated and both had more freely available dense undergrowth than

241   Campbell Park, thus we consider both sites to be moderate habitat quality. Females

242   from the focal and previous study heard songs from both of these populations,

243   allowing us to determine whether there were differences when using the same

244   stimulus. The playback for a trial was chosen at random, however, if a playback was

245   used 3 times it was retired.

246

247   **Statistical Analysis**

248   To determine whether territory occupancy rates were an accurate proxy for

249   territory quality we determined the relationship between territory quality

250   (proportion of previous 8 years occupied) and fledgling production. We used a

251   Generalized Linear Model (GLM) with a Poisson error distribution; the number of

252   fledged young was the dependent variable and territory quality was the predictor.

253   We examined the relationship between territory quality, female response and

254   aspects of the social group (female age, subordinate presence, territory residency

255   (new or same as last year), or duration of social pair (new or same as last year),

256   using a GLM with a normal error distribution and territory quality as the dependent

257   variable. Response score was positively related to date ($R^2 = 0.15$, p=0.004); we

258   used the residual of response score regressed on date in all analyses as the date-

259   adjusted response score.

260

261   We contrasted female responses in the focal population with responses reported in

262   females living in high quality habitat (Cain et al. 2015). We tested for population

263   differences in each of the four behaviors used in the PC, the first PC score and pre-

264   trial song rates using five separate GLMs (Poisson error distribution). The behavior

265   of interest was the dependent variable and population was a fixed factor. We also

266   tested for a population difference in response score using after restricting the data

267   set to the sub-set of females that heard song from one of the two moderate quality

268   populations.

269

270   To test explicitly for population differences in the relationship between female

271   response and reproductive success, we used two GLMs with the reproductive

272   success estimates as the dependent variable (fledge/fail, binomial distribution;

273   number of fledglings, Poisson distribution), and age (old/young), presence of

274   subordinates (yes/no), date-adjusted response score, and all interactions with

275   response score as potential predictor variables. For all models we used backwards-

276   stepwise procedures to select variables for the final model ($P > 0.05$ to remove), we

277   also present full models for comparison.

278

279 **RESULTS**

280 *Territory quality, response, and success*

281 Territory quality (occupancy rate) was positively related to the number of fledglings

282 produced in that territory (Fig. 1a; X^2= 6.5, B=1.2, p=0.01). Further, females in better

283 territories had fewer failed nests (X^2= 3.9, B=-0.7, p=0.0048). However, territory

284 quality was unrelated to the total number of eggs laid, the number of hatchlings, and

285 the number of nestlings banded (all p>0.05).

286

287 Territory quality was negatively related to date-adjusted female response scores

288 (PC1); i.e. more responsive females were on the lowest quality territories (Fig. 1b; X^2

289 = 5.3, Estimate = -0.07 ± 0.03, P =0.02). There was no relationship between territory

290 quality and female age, subordinate presence, territory residency, or duration of

291 social pair (all P >0.05).

292

293 *Population differences in song rates, response and success*

294 The two populations showed marked differences in song rates during the pre-trial

295 and in response to the playback. Females in the focal population (Campbell Park)

296 sang at a higher rate (X^2 = 15.1, p=0.0001) and showed a more robust response to

297 the simulated territorial intrusion in all behavioral measures than females in our

298 previous study (Fig. 2; Trial song rate, X^2 = 13.6, p=0.0002; Flights, X^2 = 18.7,

299 p<0.0001; Time within 5m, X^2 = 767, p<0.0001; Latency, X^2 = 722, p<0.0001).

300 Consequently, response scores (PC1) also differed by population, higher in this

301 study (n=24) than in the previous study population (n=28) (Fig. 2, X^2= 12.3,

302 p=0.0005). This population difference persisted when examining only the sub-set of

303   females that heard playbacks from the moderate quality habitat populations (CP, n=

304   7; BG, n=10) (X^2= 8.8, p=0.0029).

305

306   In the full model examining the potential drivers of response across the two

307   populations we found that response score (PC1) was not statistically related to age,

308   territory residency (new or old), age of social pair (new or same as last season), or

309   the presence of subordinates (all p>0.30). Date of trial and population were the only

310   significant predictors of response (Final model X^2 = 25.7, p<0.0001; Population, *B*= -

311   0.73, SE ± 0.16, p <0.0001; Date of trial, *B*=3.70e-7, SE ± 9.5e-8, p=0.0002).

312

313   Explicitly testing for population differences in the relationship between response

314   and estimates of reproductive success revealed no fixed effect of response score or

315   population on reproductive success (summarized in Table 1). However, there was

316   an interaction between response score and population. High response scores were

317   associated with more fledglings and improved nest success in the previous study

318   (BG, high quality habitat), while high response scores in females in the current study

319   (CP, low quality habitat) were associated with reduced fledgling production and

320   nest success (Table 1; Fig. 3).

321

322

DISCUSSION

We examined the relationship between competitive trait expression (response to simulated intruder), resource acquisition (territory quality), and reproductive success estimates (nest success and number of fledglings) in a population of superb fairy-wrens that resides in low quality habitat with a patchy distribution of quality nest sites. We found that the intensity of response was much stronger in the focal population than the response of females residing in high quality habitat, reported in a previous study (Cain et al. 2015). Further, we found that in this study, more strongly responding females occupied lower quality territories and had reduced reproductive success. Together, these findings suggest that differences in resource availability may have important consequences for competition intensity, how selection acts on female behavior, and female-female contest rules.

Territory quality and response

Social selection predicts that an intense response to intruders will be associated with elevated competitive ability, which may be favored in a competitive environment if it results in better access to high quality or limited resources. For instance, in tree swallows (*Tachycineta bicolor*), female response to a simulated intruder positively predicts whether a female will be able to acquire a nesting cavity (Rosvall 2008). Similarly, aggressive female eiders (*Somateria mollissima*) were more likely to attain a central position for their young in unrelated multi-brood groups, decreasing their predation risk (Öst et al. 2007). Female European starlings (*Sturnus vulgaris*) with more intense responses to intruders are more likely to be

346 monogamously mated, and thus monopolize paternal assistance (Sandell 1998).

347 Few studies have directly examined female song and fitness, however, in New

348 Zealand bellbirds (*Anthornis melanura*), female song rate and complexity were both

349 positively related to reproductive success (Brunton et al. 2016), and previous work

350 in a population of superb fairy-wrens occupying more uniform, high quality habitat,

351 also found a positive relationship between female response to an intruder and

352 reproductive success pattern (Cain et al. 2015), suggesting that intense response

353 may be related to ability to acquire and defend a high quality territory, i.e.

354 competitive ability.

355

356 In contrast, in the current study we report that in a different population, during the

357 same breeding season, high responding females occupied lower quality territories,

358 and likely as a by-product, had reduced reproductive success. One explanation for

359 this finding is that a heightened response to a competitor may be detrimental to

360 female fitness in some contexts, as has been suggested for female ornaments

361 (Nordeide et al. 2013; Swierk and Langkilde 2013). Previous work in other species

362 has shown that female responsiveness can be costly, particularly in terms of

363 maternal care (Bell et al. 2011; Rosvall 2011b; Nelson-Flower et al. 2012; Cain and

364 Ketterson 2013). For example, in dark-eyed juncos (*Junco hyemalis*) and tree

365 swallows, aggressive females often have lighter nestlings, and spend less time caring

366 for offspring (Rosvall 2011b; Cain and Ketterson 2013). In Southern pied babblers

367 (*Turdoides bicolor*), females aggressively suppressing subordinate female

368 reproduction suffered costs in terms of reproductive success (Nelson-Flower et al.

369 2012). If food availability is limited on low quality territories, then this cost may be

370   exaggerated as females are forced to trade-off territory defense with food

371   acquisition, whereas females that invest less in defense and occupy territories with

372   higher food availability may face less of a trade-off in terms of time and energy

373   available for investment in offspring. Finally, recent work on a separate study

374   system of superb fairy-wrens found that individual females suffer higher predation

375   rates when they have high song rates in or near the nest (Kleindorfer et al. 2016),

376   suggesting an additional cost to female song.

377

378   A second potential explanation is that low levels of resource availability alter

379   female-female contest rules (Enquist and Leimar 1987; Grafen 1987; Lindström and

380   Pampoulie 2004). When individuals achieve reproductive success or survival only if

381   they can acquire and defend a scarce resource, the costs of not defending may be

382   higher than the costs of fighting against higher quality individuals or escalating the

383   fight (Smith and Parker 1976). This phenomenon has been termed a 'divisive

384   asymmetry' (Grafen 1987; Tibbetts 2008; Elias et al. 2010). Female-female contest

385   competition is generally less well-studied than male-male contest competition, but

386   the available data suggest that divisive asymmetries may be more common in

387   females than males (Draud 2004; Tibbetts and Shorter 2009; Elias et al. 2010;

388   Rosvall 2011a). This sex difference may be due to differences in the nature of the

389   resources that females compete over (Clutton-Brock 2009; Elias et al. 2010; Rosvall

390   2011a; Stockley and Bro-Jørgensen 2011). In jumping spiders (*Phidippus clarus*),

391   male contests are focused on mate acquisition and signaling is correlated with size

392   and mass. In females, competition is focused on refuges and signaling is unrelated to

393   size; female-female contests are determined by resource value (Elias et al. 2010).

394   Similarly, in Texas cichlids (*Herichthys cyanoguttatum*), size determines the

395   outcome of male, but not female contests (Draud 2004). In each case, the value of

396   the resource is higher, and the consequences of losing the contest are more severe,

397   for females than for males. For instance, in the jumping spider, a male that loses a

398   confrontation may lose a mating opportunity but a female that loses a contest risks

399   death (Elias et al. 2010). This possibility is further supported by experiments in

400   paper wasps (*Polistes dominulus*), which found that females respect differences in

401   signaling or size when the value of a resource is low, but when a resource value is

402   high, females disregard signals of competitive ability and will escalate contests

403   (Tibbetts 2008).

404

405   Such extreme consequences may lead to lower quality individuals showing

406   heightened aggression when forced to defend resources, a phenomenon termed the

407   "desperado effect" (Grafen 1987). This can lead to females escalating contests and

408   risking injury or death, despite the opponent being larger or of higher quality. For

409   example, female jumping spiders will escalate contests over hibercula (refuges) to

410   the point of injury or death, ignoring differences in size and mass. Further, females

411   that were closer to molt time, and thus less likely to find another hibercula, were

412   more likely to win (Elias et al. 2010). Though female aggression in fairy-wrens is

413   usually expressed via song and chasing, female have been observed pinning other

414   females to the ground and pecking them repeatedly, often in the direction of the

415   eyes (Mulder 1995 and KEC personal obs.). The heightened aggression we observed

416   in females on lower quality territories might be a product of this desperado effect. In

417   superb fairy-wrens, males often remain on or near natal territories as subordinates

418 and are able to father extra-pair offspring and queue for a breeding position in later

419 years (Cockburn et al. 2009). Thus, males are able to survive and reproduce even

420 though they do not acquire a territory in their first year. In contrast, daughters

421 disperse off their natal territory, and any female that fails to acquire a territory and

422 mate has a fitness of zero; she dispersed to her death with no reproductive success

423 (Cooney and Cockburn 1995; Cockburn et al. 2003). Consequently, female mortality

424 is very high in the first year of life, resulting in a male-biased sex ratio (Cockburn et

425 al. 2008). Females occupying low quality territories, may be more willing to take

426 risks and express elevated levels of aggression, regardless of the costs, because the

427 consequences of losing that territory are so extreme (death and no reproductive

428 success), and they have reduced future fitness expectations (Smith and Parker 1976;

429 Grafen 1987; Cooney and Cockburn 1995; Wolf et al. 2007). In contrast, females that

430 are higher quality themselves, or occupy higher quality territories, may be more risk

431 averse and less likely to escalate (Wolf et al. 2007).

432

433 *Population differences in female response*

434 Territory defense is a costly behavior, requiring significant time and energy, and

435 increasing the risk of injury or death (Emlen and Oring 1977; Grant 1993; Nelson

436 2005). However, monopolizing limited resources can improve survival and

437 reproductive success (Nelson 2005; Rosvall 2011a; Stockley and Campbell 2013).

438 When resources are more limited, or clumped, the benefits increase relative to the

439 costs, while uniform distribution or high density of competitors reduce the benefits

440 (Grant 1993; Grant and Guha 1993; Noël et al. 2005). Experiments examining these

441 relationships in fish and birds support these general predictions (Grant 1993; Grant

442   and Guha 1993; Goldberg et al. 2001; Noël et al. 2005). There are few data

443   examining how this pattern applies to female-female competition for reproductive

444   resources, but the overall pattern is similar. Female-female competition is generally

445   elevated when critical resources are limited, but attenuated when resources are

446   more freely available. For example, in Soay sheep (*Ovis aries*) (Robinson and Kruuk

447   2007) and South American sea lions (*Otaria flavescens*) (Cassini and Fernández-

448   Juricic 2003), aggressive female interactions are most frequent when resources

449   were limited. Our results also support this prediction, we found that females in

450   patchy habitat with low density of quality territories showed much stronger

451   responses to a simulated intruder than females occupying fairly uniform, high

452   quality habitat (Cain et al. 2015).

453

454   The two populations also differed markedly in density; the high quality habitat

455   (previous study) had roughly double the density observed in the low quality

456   population (current study). Resource defense theory predicts a dome-shaped

457   relationship between the density of competitors and the level of aggression such

458   that aggression should be highest at an intermediate level of competitor density

459   (Grant 1993; Noël et al. 2005). Females in the high density/quality population may

460   experience a higher rate of female intruders prospecting for potential territories

461   and need to minimize the amount of time and energy devoted to responding to

462   intruders (Grant 1993; Noël et al. 2005). If so, they may be less likely to respond

463   strongly until it is clear that the intruder intends to settle and is actually a threat.

464   Similarly, females in the low density/quality population may experience relatively

465   few prospectors, and thus may be capable of responding to all prospectors as a

466   serious threat with less of a time and energy tradeoff than females face in high

467   quality habitat. Research in examining competition in two species of fish, convict

468   cichlid juveniles (*Archocentrus nigrofasciatus*) and male Japanese medaka (*Oryzias*

469   *latipes*), support this possibility (Grant 2000; Noël et al. 2005). However, previous

470   research in female stripe-headed sparrows (*Aimophila r. ruficauda*) showed an

471   increased response when subjected to repeated intrusions (Illes and Yunes-Jimenez

472   2009). Due to a lack of research, it is currently unclear which pattern is more

473   general and why we observe differences. Regardless, these findings suggest that

474   habitat quality and resource availability are likely important factors shaping female

475   phenotype.

476

477   A final possibility is that the observed population difference is an artifact of our

478   experimental procedure. To avoid the song of a neighbor we used songs recorded in

479   another population. As a result, some females in the high quality habitat (BG) heard

480   songs recorded from females in low quality habitat (CP), and vice versa. If BG

481   females are of higher quality than CP females, and singer quality is reflected in the

482   song, females may respond differently according to the quality of the singer. This

483   may partially explain the observed population difference. Though it is not currently

484   clear whether female song indicates individual or territory quality in fairy-wrens,

485   research suggests it is possible. In an island population of superb fairy-wrens, song

486   length is correlated with female size, though not other measures of quality

487   (Kleindorfer et al 2013). In other species some song parameters relate to age

488   (Langmore et al. 1996; Pavlova et al. 2010). In male silvereyes (*Zosterops lateralis*),

489   experimentally supplementing food increased the quality and quantity of their

490   songs (Barnett and Briskie 2006).

491

492   Although we found that the population difference in response persisted even

493   when examining responses to the same stimuli (moderate quality populations),

494   relative quality is likely to be more important that absolute quality (Young et al.

495   2015). Females in high quality habitat (BG) may perceive the same stimuli as less of

496   a threat because they are higher quality themselves. However, while female African

497   black coucals (*Centropus grillii*) adjust their response according to the threat level of

498   the song, they do so by responding more cautiously to high quality song (Geberzahn

499   et al. 2010). Similarly, female American goldfinch (*Spinus tristis)* avoid foraging near

500   models with bright bills, i.e. dominant females (Murphy et al. 2009) . If the same

501   phenomenon underlies the pattern we report, it would suggest that females in the

502   low quality habitat are singing the most threatening songs. Further, while this

503   quality difference may explain the population difference in response, it would not

504   explain the observed population difference in basal song rates, or the population

505   difference in the direction of the relationship between response and reproductive

506   success. Regardless, the role of female quality in contests has received little

507   attention and future studies should consider asymmetries between signaler and

508   receiver in greater detail. Further, research is needed to clarify the mechanisms

509   determining how female quality mediates settlement patterns, e.g. do high quality

510   females settle on high quality territory.

511

512   *Context-dependent relationships*

513   Together with previous work, the available data suggest that selection on female

514   competitive traits, i.e. the relationship between trait value and reproductive success,

515   is context dependent. We advise caution in using data from two populations to draw

516   strong inferences regarding the mechanisms driving the observed population

517   differences in selection regimes. However, other studies have found similar context

518   dependent relationships between female competitive trait expression and

519   reproductive success. In female northern elephant seals (*Mirounga angustirostris*),

520   older, more dominant females had greater reproductive success, but the pattern was

521   most evident when population density was high (Reiter et al. 1981). In black-

522   throated blue warblers (*Dendroica caerulescens*), there were strong positive age

523   effects on reproductive success in high-quality habitat, but the effect was attenuated

524   in low quality habitat (Holmes et al. 1996). In dung beetles, female fitness is reduced

525   when females have to compete, but the reduction is most evident in smaller, less

526   competitive females (Watson and Simmons 2010). These studies echo the pattern

527   we reported in the high-density population (Cain et al. 2015). Context dependent

528   relationships were also observed in dark-eyed juncos; more aggressive females

529   produced smaller eggs and hatchlings in some years, but also had greater nest

530   success in some years (Cain and Ketterson 2012, 2013). Similarly, studies examining

531   the consequences of dominance and aggression in female primates find strong

532   benefits in some species and populations, while others find no effect (Packer et al.

533   1995). In female agaonid fig wasps, some species exhibit lethal aggression, while

534   closely related species do not, and the difference appears to be explained by

535   resource availability (Dunn et al. 2014).

536

537   The context dependent nature of these relationships suggests that the selective

538   forces shaping female competitive trait expression are complex. Detailed

539   examinations of the relationship between trait expression and fitness at different

540   levels of resource availability and competitor density are necessary if we are to

541   understand how selection might shape female phenotypes and female-female

542   contest rules (Cain and Rosvall 2014). Often female contests and trait expression are

543   assumed to operate in a manner analogous to what has been reported in males.

544   However, given the sex differences in the nature of same-sex competition there is no

545   reason to assume this is true (Trivers 1972; Draud 2004; Elias et al. 2010). For

546   instance, many sexually selected traits are condition-dependent (Cotton et al. 2004;

547   Siefferman et al. 2005; Grunst et al. 2014); if female territorial response were

548   condition-dependent we would expect higher levels of trait expression in the high

549   quality population, while we observed the reverse pattern.

550

551   Importantly, we examined the relationship between response and reproductive

552   success only in territory holding females. There are females that disperse but fail to

553   acquire territories and die before breeding (Cooney and Cockburn 1995; Mulder

554   1995). In the current analysis, only females that occupy a territory were included in

555   the study, and those that achieved no reproductive success for the season appear to

556   have no fitness. Acquiring a territory, even if it is low quality and results in no

557   reproductive success in one season, still provides a pathway for females to survive

558   and the chance to breed the following season, perhaps in a better territory is a

559   vacancy occurs. Thus, it may be that a high level of aggression is necessary to

560   acquire a territory at all, which would impose strong positive directional selection

561   before reproduction begins (West-Eberhard 1983). Whether this is occurring in

562   fairy-wrens is difficult to determine, but research in tree swallows supports this

563   possibility; only the most aggressive females were able to win a nesting cavity, and

564   thus high levels of aggression were needed to even attempt breeding (Rosvall 2008).

565   Territory defense behaviors can also have important consequences for survival,

566   particularly in resident species and in the non-breeding season, when competitive

567   ability may influence access to food and cover (Ketterson 1979; Marra 2000;

568   Robinson and Kruuk 2007). Viability selection could therefore neutralize or

569   exaggerate the apparent costs and benefits of female response behavior (Cain and

570   Rosvall 2014).

571

572   *Conclusion*

573   Female competition and female expression of competitive traits are a common but

574   poorly understood phenomenon. Our results, in conjunction with previous work,

575   suggest that the rules of female-female competition may be complex and quite

576   different from the rules we observe in male-male contests. Further study into how

577   the nature of the limited resource, the consequences of losing contests, and resource

578   distribution influence female fitness is critical for understanding how changes in

579   ecology may shape female phenotypes.

580

25

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778

FIGURES CAPTIONS

781 **Fig. 1** Panel A: Territory quality, calculated as the proportion of years between 1999 and

782 2011 the territory was occupied, and number of fledged young; line is a regression from

783 a generalized linear model with Poisson distribution. Panel B: Territory quality and

784 response towards a simulated intruder (song and activity in response to novel female

785 song in territory), line is from a linear regression.

786

787 **Fig. 2** Population differences in number of songs, number of flights, time spent within

788 5m of playback, latency to respond, and overall response scores observed in response to

789 a simulated intruder. Light grey bars are responses from females in the previous study

790 population, occupying fairly uniform and high quality habitat; dark grey bars are

791 responses from females in the current study population, occupying patchy, low quality

792 habitat. Low latency indicates a more rapid response to the threat. The bold central line

793 represents the median, boxes the interquartile range (25–75 %), and whiskers the 90th

794 percentile.

795

796 **Fig. 3** Relationship between female response to a simulated intruder and estimates of

797 reproductive success, according to population. Panel A: Relationships between date-

798 adjusted response scores and nest success. Lines are population specific logistic

799 regressions estimating the probability that a female with a given response score will

800 produce a successful nest for a given response score. Panel B: Relationships between

801 date-adjusted response scores number of fledglings produced; lines are population

802 specific regressions. Some points in both panels are jittered for clarity.