

1 **Integrating fitness components reveals that survival costs outweigh other benefits and costs of**
2 **group living in two closely related species**

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25 Main text

26 Appendix A

27 **Abstract**

28 Group living can be beneficial when individuals reproduce or survive better in the presence of
29 others, but simultaneously there might be costs due to competition for resources. Positive and
30 negative effects on various fitness components might thus counteract each other, so integration is
31 essential to determine their overall effect. Here, we investigated how an integrated fitness measure
32 (reproductive values; RV) based on six fitness components varied with group size among group
33 members in cooperatively-breeding red-winged and superb fairy-wrens (*Malurus elegans* and *M.*
34 *cyaneus*). Despite life history differences between the species, patterns of RVs were similar,
35 suggesting that the same behavioural mechanisms are important. Group living reduced RVs for
36 dominant males, but for other group members this was only true in large groups. Decomposition
37 analyses showed that our integrated fitness proxy was most strongly affected by group size effects
38 on survival, which was amplified through carry-over effects between years. Our study shows that
39 integrative consideration of fitness components and subsequent decomposition analysis provide
40 much needed insights into the key behavioural mechanisms shaping the costs and benefits of group
41 living. Such attribution is crucial if we are to synthesize the relative importance of the myriad group
42 size costs and benefits currently reported in the literature.

43 **Introduction**

44 Individuals often derive benefits from living in groups but may also suffer costs derived from the
45 presence of others. Individuals may survive or reproduce better in groups, for example because living
46 in groups can increase foraging success (Stander 1992), facilitate thermoregulation (Gilbert et al.
47 2009) and provide protection against predators (Hamilton 1971; Sorato et al. 2012). Sometimes group
48 members even assist in raising each other's offspring (Brown 1987; Koenig and Dickinson 2016),
49 which can increase current reproduction (Emlen and Wrege 1991; Koenig and Walters 2011) or reduce
50 the workload and thereby increase subsequent parental survival (Meade et al. 2010; Paquet et al.
51 2015). However, group members can also affect fitness negatively as the presence of extra group
52 members can increase intra-specific competition for resources (Newton 1992), which might result in
53 increased stress (Markham et al. 2015), reduced mating opportunities (Heg et al. 2008; Huchard and
54 Cowlshaw 2011) and reduced survival (Brouwer et al. 2006). Furthermore, fitness may vary with
55 group size in a non-linear way, such that smaller groups may benefit from additional group members,
56 whereas larger groups may suffer a cost (Packer et al. 1988).

57 A limitation in the literature is that many studies on group living only quantify fitness cost and
58 benefits on a single fitness component, particularly reproductive success (Stacey and Koenig 1990;
59 Ebensperger et al. 2012; Koenig and Dickinson 2016). However, those studies that do consider
60 multiple fitness components, suggest that in many group living species there is evidence that various
61 cost and benefits co-occur (e.g. Chapman and Chapman 2000; Majolo et al. 2008), which may not be
62 surprising given the many mechanisms via which group members might affect each other during
63 different parts of the life-cycle. Effects of group size on one component of fitness might thus not be
64 representative for the effect group size has on overall fitness. Furthermore, some effects might be
65 more important than others. For example, fitness in long-lived species is generally much more
66 sensitive to variation in adult survival (determining the number of lifetime breeding attempts) than to
67 annual reproductive output (Clutton-Brock 1988; Newton 1989). In such situations large positive
68 effects of group size on reproduction can be easily outweighed by small—statistically hard to detect—

69 negative effects on the survival of adults. In addition, group size effects on one fitness component
70 may not be independent of that on another fitness component, and thus the costs and benefits of group
71 living may thus not be additive. For example, positive effects of group size on reproductive success
72 may only contribute strongly to overall fitness if there are no negative effects of group size on
73 offspring survival.

74 To fully understand how overall fitness varies with group size, we first need to combine
75 multiple fitness components for individuals living in various group sizes into an integrated fitness
76 measure, which thus far not been done as far as we are aware. Second, we need to quantify how the
77 effect of group size on specific fitness components contributes to how an integrated fitness measure
78 depends on group size, such that we gain a better understanding of the most important underlying
79 behavioural mechanisms shaping the costs and benefits of group living. Finally, we need to quantify
80 this for different types of group members, as individuals of different social status and sex are expected
81 to differ in the costs and benefits of group living (e.g. Clutton-Brock et al. 2006), such that the fitness
82 landscape is likely to vary across the entire range of group sizes for all type of group members.

83 Here, we combine six separate fitness components into one aggregate fitness proxy, using the
84 concept of reproductive value (RV, Fisher 1930). RV describes the expected contribution by
85 individuals of a given age- or stage-class (here group size, sex and social status) to the future long-
86 term growth of a population. Although RV is not equivalent to fitness in the sense of the change in
87 frequency of an allele, it can be seen as a useful integrated fitness proxy that can inform us about
88 optimal life history strategies (Fisher 1958; Caswell 1982; Goodman 1982; Horn & Rubenstein 1984)
89 and the strength of selection that acts on behavioural decisions that alter group size (Mumme et al.
90 1989). RVs are particularly suitable for species with a distinct age- or stage-structured life cycle, such
91 as cooperative breeders. The reason is that in such species the annual contribution of an individual in
92 a given stage class to fitness is not a simple sum of the number of gene copies contributed to the next
93 generation (year), because a breeder that survives to the next year (residual RV) is worth more than a
94 surviving offspring that will most likely become a subordinate the next year (current RV).

95 Another advantage of using this mathematical description of fitness is that it allows us to use
96 standard demographic modelling tools to perform decomposition analysis. This means we can
97 quantify for the first time how the effect of group size on one fitness component contributes to the
98 effect of group size on a proxy of overall fitness, and we can do so for different types of group
99 members (e.g. males, females, dominants, subordinates). Furthermore, by perturbing the effects of
100 group size either on a single or on multiple fitness components we can specifically test whether group
101 size effects on fitness components interact with each other in a non-additive way to determine overall
102 fitness effects, which is an unexplored area of research. Our framework is general and can easily be
103 modified to any group living species, even if fitness components are not measured across the entire
104 lifetime of individuals. Such analysis will ultimately help to determine what type of behavioural
105 mechanism—out of the myriad effects currently reported in the literature—are most important in
106 shaping the evolution of group living.

107 Our model species are the group-living and cooperatively-breeding superb fairy-wren (SFW;
108 *Malurus cyaneus*) and red-winged fairy-wren (RFWF; *M. elegans*). These species are very similar
109 in their ecology and many aspects of social organisation. In both congeneric species males are highly
110 philopatric and usually stay in their natal territory for at least one year to assist the dominant pair
111 (Rowley and Russell 1997). Most males spent their entire life on their natal territory or disperse to a
112 breeding vacancy nearby (Russell and Rowley 2000; Cockburn et al. 2008). However, the two species
113 differ in some key aspects of their life history. First, whereas female offspring also delay dispersal to
114 help in RFWF, there is obligate female dispersal in SFW and generally only those that obtain a
115 dominant position on a foreign territory are able to survive to the next breeding season (Rowley et al.
116 1988; Cockburn et al. 2003). As a result, SFW virtually never have female subordinates and their
117 group sizes are 1.5 times smaller compared to RFWF (where both sexes routinely help; see Results).
118 Second, despite both being long-lived, SFW have a lower survival than RFWF (Cockburn et al. 2008;
119 Lejeune et al. 2016), resulting in a two-fold lower life expectancy (see Results). Furthermore, RFWF
120 have a much (s)lower reproductive rate, as they only rarely rear two broods to independence in a

121 season, whereas the longer breeding season of SFW means that females of this species can raise three
122 broods to independence (Russell and Rowley 2000; Cockburn et al. 2016).

123 We predict that RVs vary non-linearly with group size because initial benefits of larger group
124 size might be outweighed by increased competition. Furthermore, we predict that how RVs depend
125 on group size will vary among different types of group members, because in both species dominant
126 males lose reproductive success to subordinates (fairy-wrens are highly promiscuous; Double and
127 Cockburn 2003; Brouwer et al. 2011), whereas dominant females gain survival benefits from having
128 subordinates (at least in SFW; Russell et al. 2007). Since a 'fast' life history should result in a greater
129 emphasis on current rather than future reproduction (Stearns 1983), the long lifespans of both species
130 suggests that effects of group size on survival will be a major factor determining the overall effect of
131 group size on RVs. Yet, the 'faster' life history of SFW should result in group size effects on
132 reproductive success being relatively more important compared to RFW. Finally, the extreme
133 philopatry means that there can be carry-over effects of group size from one year to the next. For
134 example, individuals in larger groups might reproduce or survive better and consequently may be
135 more likely to live in large groups again the next year and reap additional benefits. Here, we explicitly
136 model these transition probabilities, allowing estimation of the carry-over effects of group size.

137

138 **Methods**

139 ***Data collection***

140 RFWW data were collected in Smithbrook Nature Reserve in Western Australia (34°20'S, 116°10'E)
141 from 2008 to 2016. The main study area comprised 58-70 territories in which >99% of the adult birds
142 were individually colour-banded. Those territories were checked at least fortnightly for group
143 composition and survival throughout the breeding season (Oct-Jan) and once a nest was located this
144 was monitored bi-weekly. Nestlings were blood sampled when at least two days old to determine their
145 sex and parentage using 7 or 8 hypervariable microsatellite markers as described in Brouwer et al.
146 (2011). We use 1 November (peak breeding season) as the census date to determine the presence and
147 status of adults in the population. 88% of the border of the reserve is bounded by unsuitable habitat
148 (farmland), but three narrow corridors lead away from the reserve allowing for dispersal to the
149 surrounding state forests (Brouwer et al. 2014a). From 2009 onwards each year between 50-220
150 territories in the areas surrounding the main study area (up to 2km radius) were monitored and
151 checked for dispersers. Long-distance dispersal is extremely rare (median distance = 150m),
152 indicating that our estimates of survival are unlikely to be underestimated due to missed emigration.
153 For more details on field methods see Brouwer et al. (2011).

154 SFW data were collected at the Australian National Botanic Gardens in Canberra (35°16'S,
155 149°06'E) from 1993 to 2014. The study area comprised 55-90 territories, in which >99% of the adult
156 birds were individually colour-banded. During the breeding season (Sept-Mar) the complete nesting
157 history and performance of offspring was determined by daily census. Nestlings were blood sampled
158 when eight days old to determine their sex and parentage using 7 or 8 hypervariable microsatellite
159 markers (Double et al. 1997). We use 15 November (peak breeding season, when all young females
160 have either obtained a vacancy or died) as the census date to determine the presence and status of
161 adults in the population. Territories surrounding the study area were checked opportunistically for the
162 presence of dispersers. Note that due to obligate dispersal, female fledgling survival in SFW cannot
163 be estimated accurately and represents local survival (and thus might be underestimated, as typical

164 for non-closed populations). However, we believe this underestimation will not be strong;
165 furthermore we have no evidence that dispersal varies with group size. For more details on field
166 methods see Cockburn et al. (2003). Data are deposited in the DANS-EASY digital repository
167 <https://doi.org/10.17026/dans-2cf-ybgc> (Brouwer et al. 2019).

168 In both species, starvation of nestlings is negligible, but nest predation is high (~70%).
169 Females re-nest after failure and RFWF can initiate as many as four clutches (1-3 eggs each)
170 (Lejeune et al. 2016), but only in exceptional cases rear two broods to independence in a season
171 (Russell and Rowley 2000). The longer breeding season of SFW means that females of this species
172 can initiate up to eight clutches (1-5 eggs each) per season and raise three broods to independence
173 (Cockburn et al. 2016). Note that we compare group size effects in two populations of two related
174 species and that we discuss any differences in the context of differences in life-history among these
175 species. However, we note that these life-history differences may be due to species differences in
176 evolutionary history part as well as environmental differences among the two study sites (e.g. rainfall;
177 van de Pol et al. 2013).

178

179 *Statistical analysis of fitness components*

180 We determined six fitness components: group productivity (number of fledglings produced per group
181 per breeding season); within-group parentage (probability of paternity/maternity within own group);
182 extra-group paternity (number of offspring sired by male in other social group); offspring sex-ratio;
183 juvenile and adult survival; probability of obtaining dominant status; and the probability of
184 increasing/decreasing the group size in the next year (Table A1). Reproduction was split up into a
185 within- and extra-group parentage component, as group members can parasitize the reproductive
186 success of the dominant breeding pair (Double and Cockburn 2003; Brouwer et al. 2011).
187 Furthermore, group members can reduce constraints for dominant males to gain paternity outside the
188 social group (extra-group paternity; Mulder et al. 1994; Brouwer et al. 2017).

189 For each of the fitness components we fitted a generalized linear mixed model to the data
190 using the R statistical language (R Development Core Team 2017) and package lme4 (Bates et al.
191 2015) to estimate how each of these fitness components depended on group size. For annual group
192 productivity and number of extra-group offspring we used a Poisson model, for all other variables a
193 binomial/binary regression model. We fitted group size as fixed categorical effect to obtain the
194 maximum likelihood estimate for each level of group size for each sex and social status, while
195 including year as a random intercept to account for temporal variation. We defined group size as the
196 number of adult group members at time of census; group sizes consisting of six or more individuals
197 were lumped because only 0.2% (SFW) and 1.8% (RFW) of groups had seven or more individuals.

198 A difficulty with statistical associations between group size and fitness components such as
199 group productivity is that it is problematic to determine causality of such correlations, since high-
200 quality breeders or breeders living in high-quality territories might also produce high-quality
201 offspring and be more likely to have larger groups because of past reproductive success (Cockburn
202 1998). By studying the same individuals over multiple seasons with variable group sizes we attempt
203 to separate whether effects are due to a within-group phenotypically plastic response rather than non-
204 causal among-group correlations due to territory or group quality. We accounted for any among-group
205 covariance between group size and a fitness component by including a second group size predictor
206 variable as a linear covariate: the mean group size of the group across all years (sensu within-subject
207 centring; Snijders and Bosker 1999; van de Pol and Wright 2009). In such a model, the original group
208 size predictor variable is then assumed to reflect the within-group effect of group size on the response
209 variable.

210

211 *Reproductive values as an integrated fitness measure*

212 The aim here is to quantify the effect of the group size an individual experiences in a given year on
213 an integrative measure of fitness. Our fitness measure should be able to incorporate all above-
214 mentioned fitness components that reflect gene contributions to future generations via offspring

215 production as well as one's own survival (and future state) into a single metric, such that we can gain
216 understanding on how each of these fitness components (and associated behavioural mechanisms that
217 determine variation in these fitness components) contribute to overall effects of group size on fitness.
218 As individuals do not stay in the same group size their entire life, individual lifetime fitness measures
219 (lifetime number of offspring or $\lambda_{\text{individual}}$; McGraw & Caswell 1996) have limited value here.
220 Furthermore, formal fitness measures, such as the rate of increase of alleles (e.g. invasion fitness) are
221 practically hard to measure. Instead, we focused on the immediate (here annual) fitness impacts of
222 being in a group of specific size in a given year, by determining the contribution of individuals in a
223 given stage-class (e.g. group size) to fitness. Specifically, we used reproductive values that quantify
224 the contribution of individuals of a certain stage-class to the long-term population growth rate (Fisher
225 1930), which can be used to compare the sensitivity of fitness to events at (or behaviours affecting)
226 different (st)ages (Goodman 1982). As such, reproductive values can be used to quantify the strength
227 of selection at each stage class (and thus function as an integrated fitness proxy at each stage-class)
228 and should inform us whether behaviours that affect in which group size you live are favoured by
229 evolution (with the usual phenotypic gambit assumptions; Grafen 1984).

230 However, for species that live in groups with kin, such as fairy-wrens, indirect fitness benefits
231 also play a role (Hamilton 1964). What the optimal group size is for individuals in such a situation
232 can be better understood by considering the question whether or not it pays for an individual to accept
233 an additional group member. Specifically, Hamilton's rule (Hamilton 1964) states that natural
234 selection will favour a trait or behaviour when the direct cost (C) of a behaviour to the actor outweigh
235 the indirect benefit (B) of the behaviour to the recipient, with the benefits being weighted by the
236 relatedness r between actor and recipient ($rB > C$; the canonical version of Hamilton's rule that
237 assumes actor control and fitness additivity; Akçay & van Cleve 2016). The RVs can be used to
238 estimate the direct fitness costs and indirect fitness benefits and thereby the nett benefits ($rB - C$) of
239 the behaviour of 'accepting another group member', and this can be done for all types of actors
240 (dominant, subordinates, males, females) for different group sizes. For example, the costs and benefits

241 of accepting an additional unrelated subordinate male for a dominant male in a group size of 3 ($D\sigma_3$)
 242 can be calculated as follows. The costs will be the difference between a dominant male's RV in the
 243 current group size and his RV in a group size after accepting the new subordinate male in the group:
 244 $C_{D\sigma_3} = RV_{D\sigma_3} - RV_{D\sigma_4}$. Thus, understanding how RVs depend on group size for a given stage-class
 245 directly determines the direct costs C.

246 Similarly, the indirect benefits for the actor (A) will be the difference in RVs between group
 247 size 3 and 4 of other group members (recipients R, for example a dominant and subordinate female
 248 also present in the group) weighted by the relatedness between the actor and recipients: $rB_{D\sigma_3} =$
 249 $\sum_R (r_{A,R} B_R) = r_{D\sigma D\varphi} (RV_{D\varphi_4} - RV_{D\varphi_3}) + r_{D\sigma S\varphi} (RV_{S\varphi_4} - RV_{S\varphi_3})$. Thus, understanding how the RVs
 250 depend on group size for a given stage-class also strongly informs us about sign (and to some extent
 251 strength) of the indirect benefits B for the decision to accept additional group members. For example,
 252 if RVs of other group members are highest at group size 3, this implies that the indirect fitness benefits
 253 of accepting additional individuals in the group will always be negative and thus selection will not
 254 favour larger groups (assuming $C \geq 0$; when considering the acceptance of a related—instead of
 255 unrelated—subordinate, the situation is more complex as the benefits also depend on the relatedness-
 256 weighted benefits to the joiner).

257 In conclusion, RV determine both the direct costs and indirect benefits, which together shape
 258 inclusive fitness. However, a full analysis of inclusive fitness considerations, which can only be done
 259 for certain behaviours/traits/alleles (e.g. accept or reject an additional group member) is not trivial for
 260 both theoretical (Akçay & van Cleve 2016) and practical reasons (Bourke 2014). Here we will focus
 261 on understanding the patterns and causes of variation in RV with respect to group size, which will
 262 provide the first crucial step towards understanding the inclusive fitness of group size decisions.

263

264 **Calculation of reproductive values**

265 RVs were calculated from population matrices, which were derived from a life cycle model. We
 266 explain the main rationale of our calculations here, the exact derivation is described in appendix A.

267 We first created a life-cycle model (fig. 1a) that describes (i) the main life-history stages of our study
268 systems (dominants [D], subordinates [S], offspring [O]) and (ii) the fitness components that
269 determine transitions between these stage (the number of fledglings produced (group productivity),
270 multiplied by fledging survival until the next breeding season; annual adult survival for subordinates
271 and dominants; and transition rates (conditional on survival) among states, i.e. the probability that a
272 fledgling, subordinate or dominant will be a dominant the next year. This life-cycle model was
273 extended to also describe group size structure (fig. 1b), as we expected that most fitness components
274 depended on group size and we could model the transition probability that a group changes size
275 between breeding seasons, which allows for including carry-over effects of group living between
276 years into the residual RV. Next, the model was extended to include two sexes, sex-specific fitness
277 components as well as an offspring sex-ratio parameter (fig. A1). Finally, we split up reproduction
278 into a within- and extra-group parentage component to account for the fact that promiscuity levels
279 are group-size dependent as well (Appendix A). We note that in our model fitness components are
280 locally density dependent (i.e. group size effects), but we were unable to include any global density
281 regulation as we do not have a proper understanding yet of how this complex process acts in these
282 species (see Appendix A).

283 The next step was then to translate our life-cycle graph into a matrix population model, in
284 which the matrix elements consist of the six fitness components in which we are interested. We used
285 the statistical model estimates of each fitness component derived from the field data as input to the
286 projection matrix, which allows—using standard matrix algebra (Caswell 2001)— calculating the
287 RVs of individuals as a function of their status, sex and group size (see Appendix A).

288 To quantify the amount of uncertainty in the estimates of RVs, we performed bootstrap
289 analyses on the uncertainty of the input parameter estimates of each individual fitness component.
290 We generated 1,000 bootstrap values based on the regression models used to analyse the association
291 between group size and each fitness component. The mean and S.D. of the 1,000 bootstrap values
292 were set to be equal respectively to the maximum likelihood estimate and the S.E. of the parameter

293 on the scale of the link-function used in the regression (for details see appendix A). For each bootstrap
294 input parameter set we calculated the corresponding RVs, and by repeating this for all bootstrap sets,
295 we derived confidence intervals around the RVs.

296 It should be noted that we consider group-size driven variation in fitness components,
297 independent of the statistical p-value of any group-size effect. The reasons for this is that we deem
298 the maximum likelihood estimates for each fitness component for a given group size class to be the
299 best estimator we have available, and thus best to be used in the overall fitness model. Moreover,
300 including or excluding group size driven variation in fitness components based on an arbitrary
301 threshold p-value ignores the fact that (i) there is a continuous gradient of statistical support, (ii) we
302 expected non-linear relationships, which are hard to fit given the limited range in group size and many
303 possible non-linear shapes, and (iii) that the statistical power to detect group size effects will vary
304 across fitness components (e.g. statistically small effects of group size on survival will be hard to
305 detect, but may have large biological consequences for integrated fitness). Finally, by bootstrapping
306 from the standard errors of all parameter estimates, we directly translate all information about
307 parameter imprecision to the RV values.

308

309 ***Decomposing how the effect of group size on each fitness component contribute to effects on***
310 ***reproductive values***

311 To decompose how group size-effects on specific fitness components contribute to the overall effect
312 of group size on RV we used a model-based thought-experiment. In turn, each of the six fitness
313 components was made independent of group size by setting the value for that fitness component to
314 the (weighted) mean value across all group sizes (left panel fig. 2). Each time a fitness component
315 was made independent of group size, new RVs were calculated for each type of individual for each
316 group size: e.g. $RV_{D\sigma s, f_i(\cdot)} = RV_{D\sigma}[f_i(\cdot), f_{other}(s)]$, with $f_i(\cdot)$ being the fitness component of interest
317 that is made independent of group size, and $f_{other}(s)$ being the other five group size dependent fitness
318 components (with group size dependency as quantified in the empirical data). Subsequently, we

319 calculated the difference between the group size effect on these perturbed RVs and the group size
 320 effect on the original RV estimates (i.e. Δ in right panel fig. 2). Specifically, we quantified the
 321 contribution Δ (in units of RV/additional group member) of the group size effect of fitness component
 322 f_i to the group size effect on the RV of dominant males as: $\Delta_{RV_{D\sigma}, f_i(\cdot)} = \beta_{RV_{D\sigma}, f_i(\cdot) \sim s} -$
 323 $\beta_{RV_{D\sigma} \sim s}$, with β being the linear regression slope coefficient of the given function.

324 In addition, we also calculated the combined contribution of all underlying group size effects,
 325 by making all six fitness components independent of group size simultaneously: $\Delta_{RV_{D\sigma}, f_{1-6}(\cdot)} =$
 326 $\beta_{RV_{D\sigma}, f_{1-6}(\cdot) \sim s} - \beta_{RV_{D\sigma} \sim s}$. By comparing the combined contribution of all six fitness components to
 327 the sum of the separate contributions of all six individual fitness components ($\sum_{i=1}^6 \Delta_{RV_{D\sigma}, f_i(\cdot)}$), we
 328 can determine whether effects of group size on fitness components affect RVs in an additive way.

329 As RVs initially increased from group size two to three and then decreased (roughly linearly)
 330 with larger group sizes (see Results), decomposition analyses were done in two parts to align the
 331 application of a linear decomposition to a non-linear change with RV. We first calculated contributions
 332 for the effect of one additional group member when no (other) subordinates were present (i.e. pairs
 333 vs. group size three, except for subordinates which do not occur in pairs and thus group size three (no
 334 other subordinate) was compared to group size four (one other subordinate)). Second, we calculated
 335 contributions for the effect of additional group members when looking at groups that were size three
 336 or larger.

337

338 **Results**

339 *Life-history differences between Superb and Red-winged fairy-wren*

340 In RFW group sizes were nearly 1.5 times larger than in SFW (mean no. male subordinates per
 341 group RFW vs. SFW: 1.05 vs. 0.57; mean no. female subordinates per group RFW vs. SFW: 0.56
 342 vs. 0.002; fig. 3a & b). Further, SFW have a much ‘faster’ life-history than RFW. SFW produced
 343 on average 2.7 times as many fledglings per group compared to RFW (fig. 3c & d), and also showed
 344 much lower annual juvenile and adult survival than RFW (fig. 4a & b), implying a two-fold

345 difference in adult life-expectancy from fledging. In SFW, females generally obtained a dominant
346 position within their first year of life, or they died (fig. 4c). Many male fledgling SFW were able to
347 obtain a dominant position within their first year of life too, whereas this was extremely rare for
348 fledgling RFWW of either sex (fig. 4c & d). In both species there was a strong positive relationship
349 between group size from one year to the next, except for female fledglings in SFW, which often end
350 up in a pair after obligatory dispersal from their natal group (fig. 4e & f). Patterns of genetic parentage
351 were remarkably similar among both species (fig. 4g-j): most offspring are sired by extra-group
352 males, followed by within-group dominant and subordinate males; particularly in RFWW subordinate
353 females can gain some within-group maternity through plural breeding, which involves initiating a
354 second nest on the territory.

355

356 *Associations between group size and fitness components*

357 As explained in the Methods, we describe the patterns between each of the fitness components and
358 group size, independent of their statistical significance (but more than half of the associations were
359 significant when fitting linear or quadratic regression; see table A2). Group productivity increased
360 with group size in SFW, but not in RFWW (fig. 3c & d). For some other fitness components a few
361 extra group members were beneficial, whereas larger group sizes reduced the benefits. In SFW this
362 was true for survival of all group members, except dominant males (fig. 4a) and the number of extra-
363 group offspring sired by dominant males (fig. 4i). RFWW followed a somewhat similar, but more
364 erratic pattern for survival (fig. 4b).

365 Other fitness components were negatively associated with group size. In both species, the
366 proportion of within-group paternity of dominants declined with group size (fig. 4g & h). Dominant
367 males in larger groups were also less successful in siring extra-group offspring, particularly in RFWW
368 (fig. 4j). In both species, dominant males tended to have somewhat lower survival in the presence of
369 a single subordinate than in pairs, whereas survival slightly increased again for larger groups (except
370 for group size 6+ in SFW, but note the large S.E.s which stem from small sample sizes, further note

371 that none of these patterns is significant; fig. 4a & b). The probability that subordinates recruit to a
372 dominant position decreased with increasing group size, but it increased again with very large group
373 sizes in SFW (fig. 4c & d).

374

375 *Associations between group size and integrated fitness proxy*

376 Aggregating the different fitness components into RVs showed the predicted non-linear association
377 with group size. Also as predicted, RV patterns varied among the type of individuals. Specifically, in
378 both species all group members, except for dominant males, had highest RVs in the presence of one
379 and in some cases two extra group members (fig. 4k & l), while more group members reduced RVs.
380 However, RVs of dominant males decreased in the presence of additional group members and suffered
381 substantially in large groups (fitness reductions of 41% in SFW and 28% in RFWF when comparing
382 males in groups of 6+ with those living in pairs; fig. 4k & l).

383

384 *Relative importance of group size effects via different fitness components*

385 Decomposition analyses showed that, as predicted, for both species the effects of group size on
386 survival and on the carry-over effects of group size from one year to the next were important
387 determinants of group size effects on RVs (fig. 5). Only for subordinate males and dominant female
388 SFW living in groups without (other) subordinates something other than the survival effect was more
389 important (filled bars fig. 5f-h). For subordinate males this was the group-size effect on recruitment,
390 and for dominant female SFW this was the effect on reproductive success (filled bars fig. 5f-h). The
391 prediction that group size effects on reproductive success would be relatively more important for RVs
392 in SFW, with a faster life history compared to RFWF, was supported for dominants, although mainly
393 for dominant females (fig. 5h). The gain and loss of paternity both within and outside the group were
394 relatively important for group size effects on RVs of dominant males (fig. 5j & k), but less so for
395 subordinate males (fig. 5f & g).

396 Finally, in both species the combined contribution of group size effects via all six fitness
397 components was typically different than the sum of the separate contributions of all six individual
398 fitness components on RV (i.e. the whole is not the sum of its parts; fig. 5 'Comb' vs. 'Sum'). This
399 difference indicates that the group size effect on one fitness component is not independent of that on
400 another fitness component, and thus that costs and benefits of group living on RVs are non-additive.
401 In general, if group size negatively affected RVs the sum of the contributions was more negative than
402 the combined effect of group size via the different fitness components on RV (fig. 5), suggesting that
403 group size effects on different fitness components dampen each other. By contrast, if group size
404 positively affected RVs the sum of the contributions tended to be less positive than the combined
405 effects of group size (fig. 5), suggesting that group size effects on different fitness components
406 intensify each other.

407

408 **Discussion**

409 Group living has many concurrent costs and benefits. However, a framework to integrate various
410 fitness components had not been previously applied to this question, and therefore it has proven
411 difficult to determine how fitness varies with group size. Here we integrated six key fitness
412 components into reproductive values (RV) and determined how these RVs varied among group
413 members and sizes in two congeneric species that have a similar ecology, but differ in some key
414 aspects of life history. As predicted, several fitness components as well as RV varied non-linearly
415 with group size. The remarkably similar patterns in how RVs varied with group size suggest that the
416 same behavioural mechanisms are important in both species. Furthermore, there was not much
417 support for our prediction that RVs of the species with a faster life history would be more sensitive
418 to effects of group size on reproductive success. For both species, the costs of additional group
419 members on survival were most important for RVs and this was amplified through carry-over effects
420 of group size between years (i.e. large groups suffer survival costs, and are likely to do so the next
421 year as well). In both species, RVs of most group members was highest in small groups (size 2-3),

422 and larger group sizes reduced RVs, whereas RVs of dominant males was highest in the absence of
423 subordinates. These results thus suggest that for most group members there are both direct costs and
424 negative indirect fitness benefits of accepting additional unrelated group members. Finally, as
425 predicted we found that how group size affects RVs varied among different types of individuals,
426 suggesting that group members potentially might have a conflict of interest over the optimal group
427 size.

428

429 *Cooperation and competition among group members*

430 How several fitness components and RVs varied with group size was quite similar among both
431 species, despite the fact that RFWF had nearly 1.5 times larger group sizes, two-fold higher life
432 expectancy and 2.7-fold lower annual reproductive success. Our findings thus suggest that in both
433 species to a large extent the same underlying demographic (and thereby likely behavioural)
434 mechanisms are important in determining how our integrated fitness measure varies with group size,
435 and is independent of life history. All group members, except dominant males, had higher RVs in the
436 presence of one or two extra group members. Both species are cooperative breeders with subordinates
437 assisting in raising offspring and previous work has already shown that this allows for load-lightening
438 in offspring provisioning behaviour (Green et al. 1995, Brouwer et al. 2014b). Living in groups might
439 also result in thermoregulatory benefits during roosting (Hatchwell et al. 2009) which could have
440 positive effects on survival, particularly because recent work in RFWF suggests that changes in body
441 condition underlie climate-related mortality (Gardner et al. 2017, 2018).

442 Interestingly, despite the initial direct benefit of living with an extra group member, our results
443 showed that the direct costs overwhelm the direct benefits in larger groups (RVs declined for larger
444 group sizes; Fig. 4). Negative effects of group size are commonly reported in group living species
445 where larger groups mean larger home ranges and thus less efficient foraging (Chapman and
446 Chapman 2000). In contrast, additional group members in cooperative breeders usually means more
447 assistance in raising offspring and relatively few empirical studies have shown that living in a large

448 group can be costly (but see: Cockburn et al. 2003; Allainé and Theuriau 2004; Brouwer et al. 2006;
449 Sparkman et al. 2011). We found that the costs of living in larger groups were the result of higher
450 competition for dominant positions and reduced survival, possibly due to increased competition for
451 food. These direct costs (and benefits) of group size might vary among years or habitats. For example,
452 in colony living cliff swallows (*Petrochelidon pyrrhonota*) larger colonies survived better in cooler
453 wetter years (Brown et al. 2016). Future work investigating spatiotemporal fluctuations in group size
454 effects could shed light on whether costs and benefits of group living vary with environmental
455 conditions.

456 As predicted, how our fitness proxy depends on group size varied among individuals of
457 different status. Notably, most group members had higher RVs in the presence of subordinates, while
458 dominant males had lower RVs in the presence of subordinates. Due to increased competition,
459 dominants lost both within- and extra-group paternity success, consistent with the idea that the
460 presence of subordinates liberates female dominants from constraints on gaining extra-group
461 paternity (Mulder et al. 1994; Brouwer et al. 2017), and subordinates parasitizing the reproductive
462 success of dominant males (Double and Cockburn 2003). This shows the significance of considering
463 the genetic offspring when calculating costs and benefits of group size. At the same time, this
464 increased competition might explain why dominant males, but not females, tended to have lower
465 survival in the presence of a subordinate compared to males in pairs. Male participation in sexual
466 competition requires costly elevated testosterone titres and dominants have higher testosterone levels
467 for longer periods of time than subordinates (Peters et al 2001). Dominants thus seem to have different
468 interests with respect to raising future group members, which suggests there may be intra-group
469 conflict over the optimal group size. Nevertheless, some of the loss of paternity will be gained by
470 related subordinates, and thus partly be compensated via indirect fitness benefits. Future work
471 calculating the inclusive fitness for different strategies (e.g. leave or stay in group) will have to shed
472 light on the relative importance of indirect fitness costs and benefits, and our framework provides a
473 crucial step in doing so.

474

475 *Relative importance of group size effects on different fitness components*

476 Decomposition analyses allowed us to determine how RVs changed as a result of group size effects
477 via underlying effects on each of the six different fitness components. The marginal—and for most
478 type of individuals, statistically non-significant—benefit of an extra group member on survival, was
479 one of the most important determinants of RVs in both species. Previous studies have emphasized the
480 expectation that group size effects on survival may be biologically most important, while statistically
481 hardest to detect (Meade et al. 2010), and our study provides a first quantitative confirmation of this
482 prediction. This result gives weight to the idea that the current focus in the literature on reproductive
483 success, may paint a non-representative picture of the overall fitness patterns, and that integrating
484 group size effects across multiple fitness components is a research priority.

485 The consistent importance of the survival pathway contradicts our prediction that effects on
486 survival are more important in a ‘slow’ life-history species and on reproductive success in a ‘fast’ life
487 history. However, although SFW had a faster life history compared to RFWF, it can still be
488 considered relatively slow compared to northern hemisphere species, which usually have much lower
489 life-expectancies (annual $P_{\text{survival}} < 50\%$; Peach et al. 2001). Furthermore, the lack of importance of
490 group size effects on reproductive success other than for female dominant SFW (in RFWF
491 reproductive success did not vary with group size), might not be surprising, since subordinates only
492 rarely sire offspring in their natal group, and the high extra-group paternity rates mean that many
493 dominant males sire offspring in other groups, which are thus unaffected by their own group size.

494 Strikingly, the carry-over effects of group size on RVs were one of the main determinants of
495 RVs. Although we hypothesized that such a relationship could be expected in group living species
496 where group size mainly depends on the number of offspring from the previous season and on the
497 survival of all group members, we have for the first time quantitatively shown that there are long-
498 term fitness consequences of being in a group of a certain size. Surprisingly, this aspect has received
499 little attention in studies of costs and benefits of group living, whereas for individuals living in viscous

500 populations choosing the right group size will not only have important current, but also future fitness
501 consequences.

502 Importantly, we showed that group size effects on different fitness components are not
503 additive. This may not be surprising given the highly complex non-linear relationships between group
504 size and each of the six fitness components. Furthermore, despite the importance of the carry-over
505 effects of group size, such an effect can only be important in the presence of another strong cost or
506 benefit, as otherwise there would be nothing to carry-over. Non-additivity thus provides another
507 reason why fitness integration is important when considering traits that might affect many different
508 fitness components simultaneously.

509

510 *Conclusion*

511 Our study shows that there can be many cost and benefits affecting different fitness components,
512 suggesting many different behavioural mechanisms play a role. These results mirror the wider
513 literature on group living that has presented many different behavioural mechanisms (see
514 Introduction). Our consideration of (i) many fitness components (ii) integrated into RVs which are
515 (iii) amenable to subsequent decomposition analysis, provides much needed insights into the key
516 behavioural mechanisms shaping the direct costs and benefits of group living in fairy-wrens. It helped
517 us see the forest for the trees, as the role of survival costs and carry-over effects of group size appear
518 to be crucial. Conducting such attribution studies more widely will be important if we are to
519 synthesize the relative importance of the myriad group size costs and benefits currently reported in
520 the literature, and our study provides a quantitative analytical framework to do so. Furthermore, our
521 approach allows for conducting subsequent inclusive fitness considerations (Hamilton 1964), and
522 thereby provides the groundwork for future studies that aim to understand what demographic and
523 behavioural mechanisms favour the evolution of cooperation or cause intra-group conflict.

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702

703

704 **Figure legends**

705 **Figure 1.** Simplified versions of the life-cycle graph used to model the effect of group size on the
706 reproductive values of individuals of different sex and status, in different group sizes. a.) Arrows
707 indicate the transition probabilities among states (Subordinates, Dominants and Fledglings)
708 determined by the fitness components: number of fledglings produced (r); probability of surviving
709 till next breeding season for fledglings (j_F); the annual adult survival for subordinates and
710 dominants (j_S & j_D); the transition rates (conditional on survival) among states (m_{FD} , m_{SD} & m_{DS}),
711 respectively the probability that a fledgling, subordinate or dominant will be a dominant the next
712 year. b.) This life-cycle can be extended to model the transition probability to move from a certain
713 group size to another (g_F , g_S & g_D , here in this example between group size 3 and 4). Note that a.)
714 and b.) are simplified versions as in our final model we included both sex differences and the range
715 of variation in group size (2-6+) in one model, see appendix A. Contributions to the next year's
716 population via different fitness component are shown in different colours (reproduction in red,
717 juvenile survival and recruitment in green, adult survival and state change in blue).

718

719 **Fig. 2.** Graphical illustration of the decomposition analyses used to determine how group size-effects
720 on each of the six fitness components contribute to the overall effect of group size on RV. The left
721 panels show how each of the fitness components (here survival and group productivity) are made
722 independent of group size. The right panels show the original (filled symbols) and newly calculated
723 RVs (open symbols), with the difference (Δ) between the two indicating the contribution of the fitness
724 component of interest to the group size-effect on RV. Note that small changes in group size effects on
725 a fitness component (e.g. survival) can have large effects on RVs.

726

727 **Fig. 3.** The relationship between group size and a. & b.) the frequency distribution of groups, c. & d.)
728 reproductive success for superb and red-winged fairy-wrens. Means are shown with their S.E.'s.
729 Numbers on top indicate the sample sizes (number of group years).

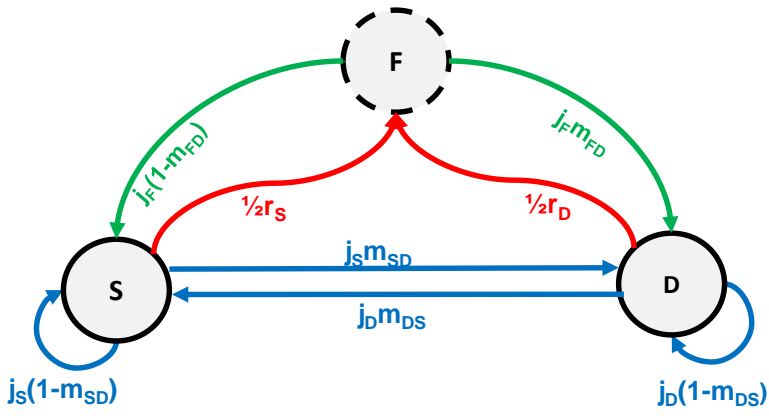
730

731 **Fig. 4.** The relationship between group size and the maximum likelihood estimates \pm S.E. of a. &
732 b.) survival, c. & d.) recruitment to a breeding position, e. & f.) group size next year, g. & h.)
733 proportion within group parentage, i. & j.) extra-group paternity (no. fledglings) and k. & l.)
734 reproductive values for superb- and red-winged fairy-wrens.

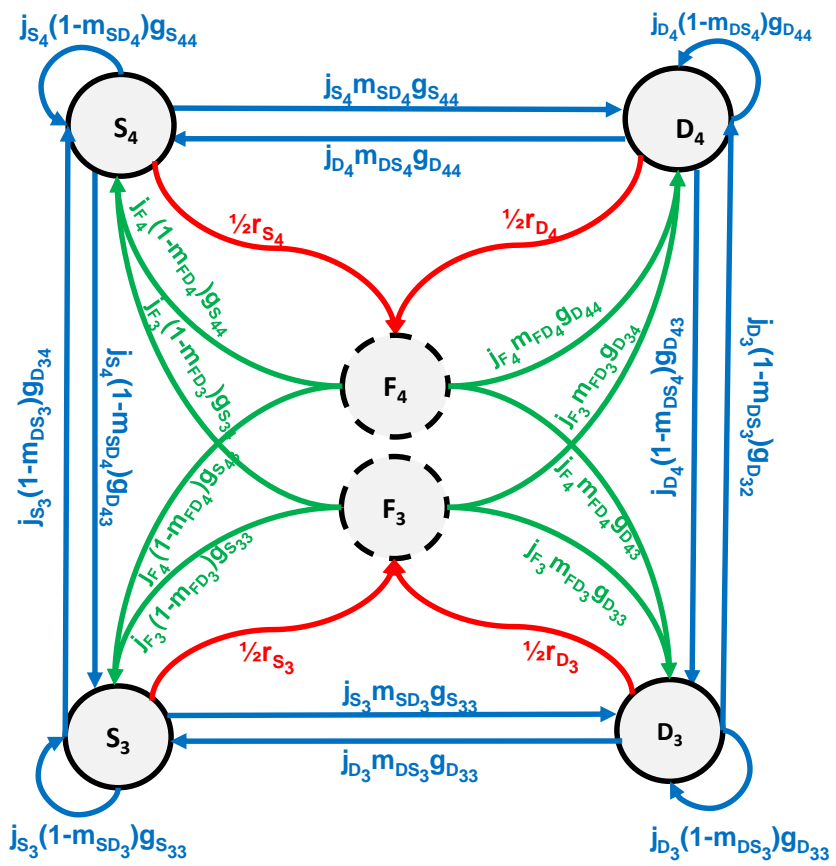
735

736 **Fig. 5.** The contribution to the group size effect on reproductive values (i.e. Δ , right panel fig. 2) for
737 six fitness components shown for the effect of an additional group member when no (other)
738 subordinates were present (filled colour) and for group size ≥ 3 (dashed colour) for superb- and red-
739 winged fairy-wrens of different sex and status. The six components are reproductive success (RS),
740 survival (Surv), recruitment to a breeding position (recr), within-group parentage (WGP), extra-
741 group paternity (EGP) and carry-over effects of group size (GS). The combined (Comb) and the
742 summed effect of the change in RV of the six fitness components (Sum) are also shown, with the
743 difference indicating the degree to which the combined effects are not additive.

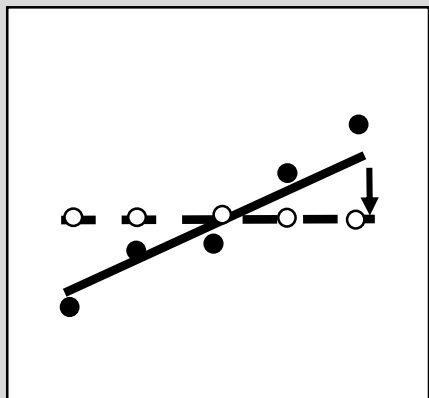
a.)



b.)

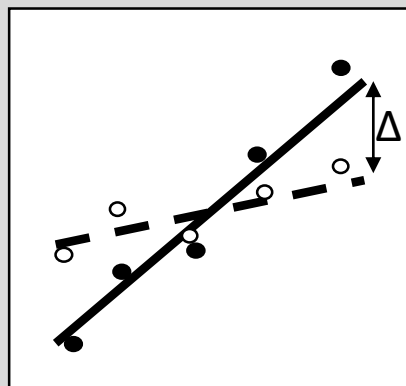


Survival



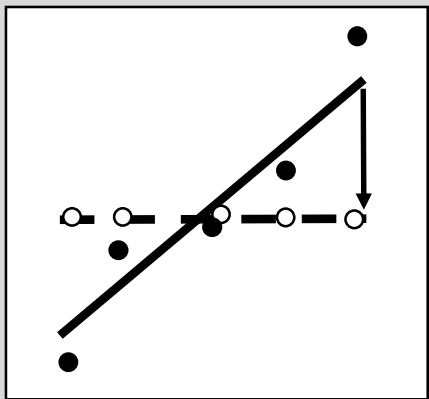
Group size

Reproductive value



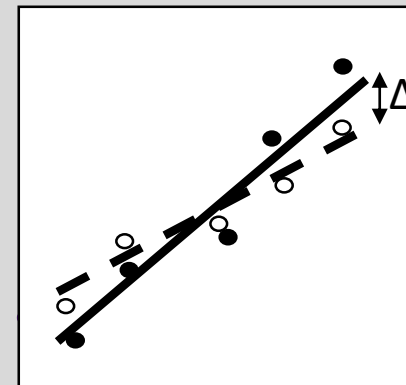
Group size

Group productivity

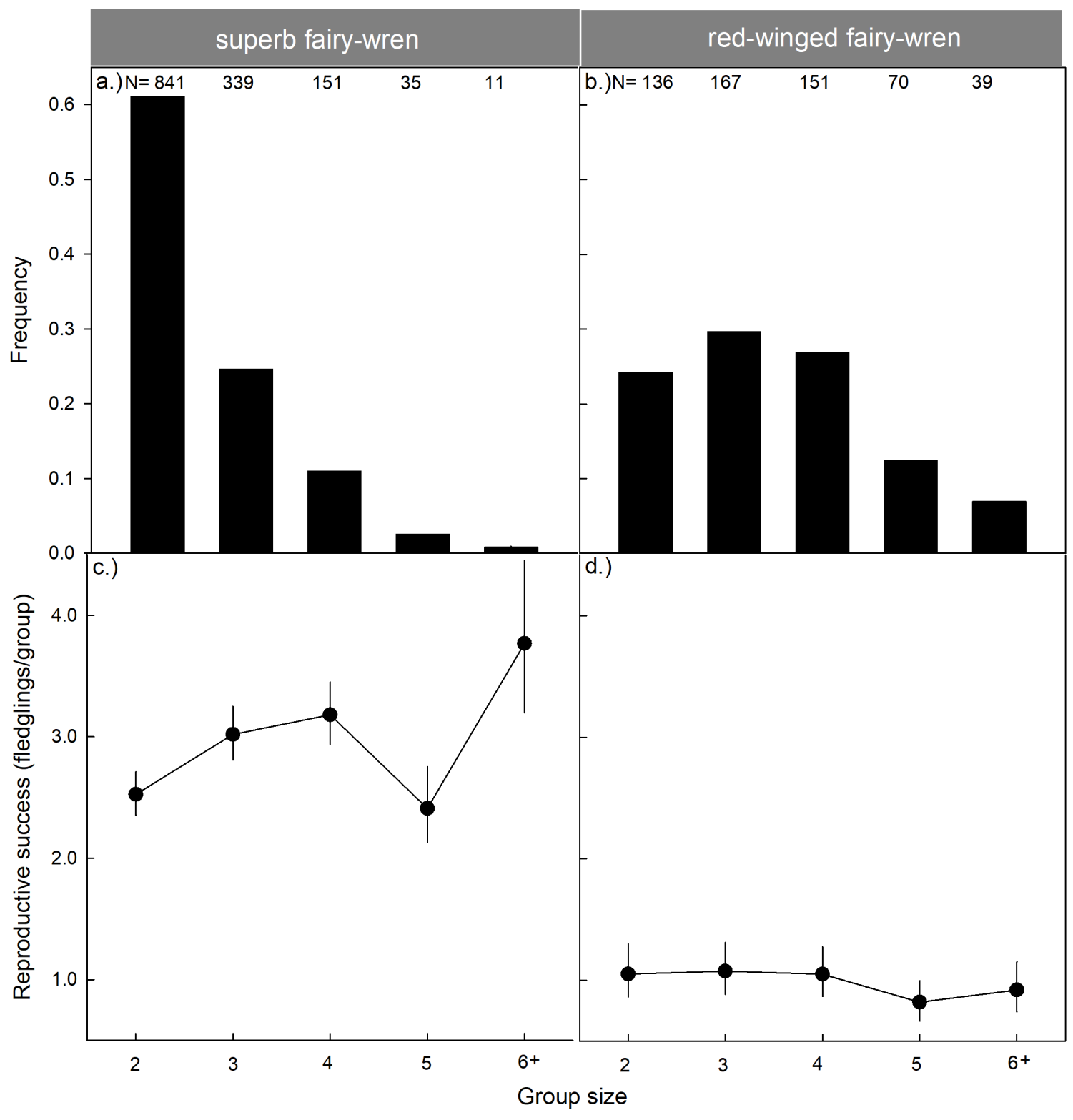


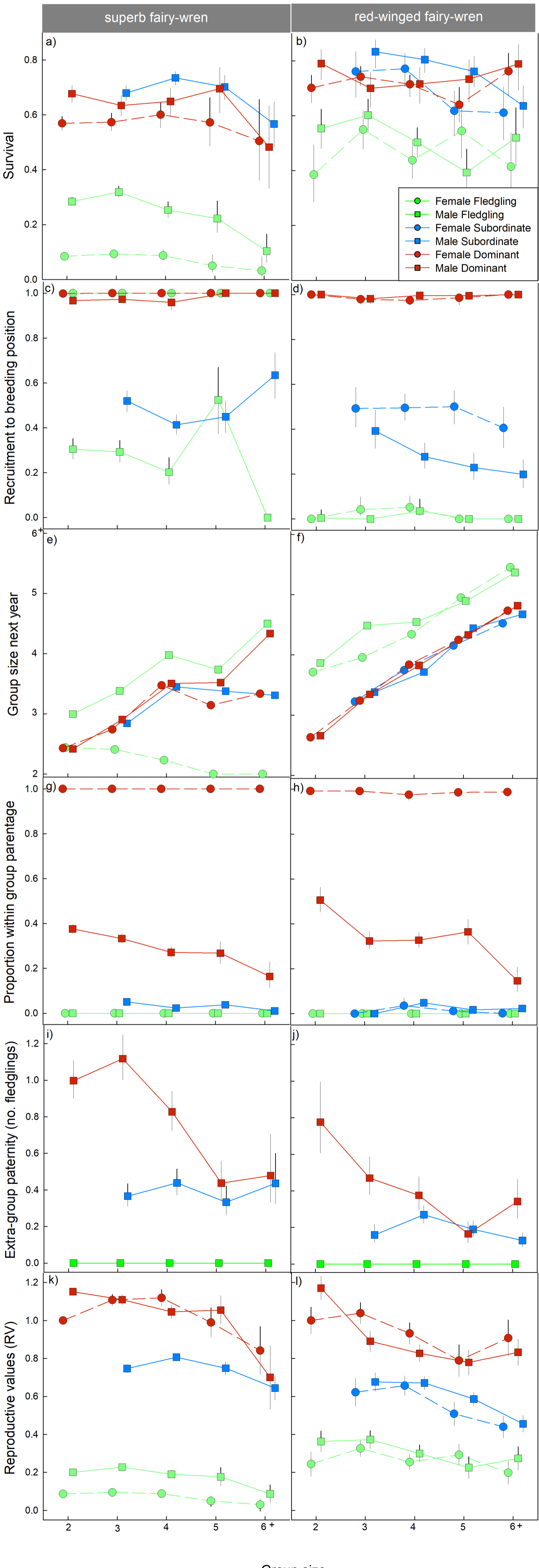
Group size

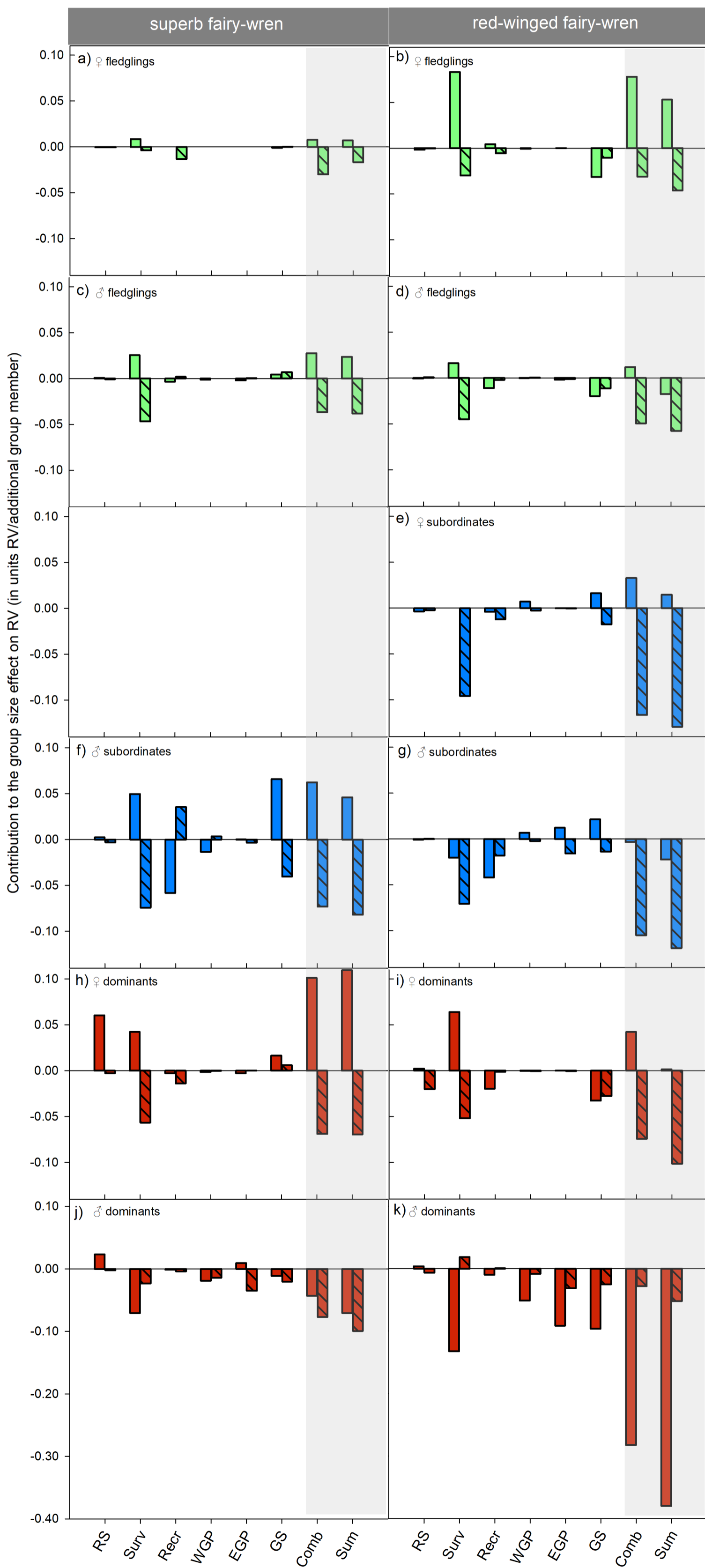
Reproductive value



Group size







1 **Appendix A of Integrating fitness components reveals that survival costs outweigh other**
2 **benefits and costs of group living in two closely related species**

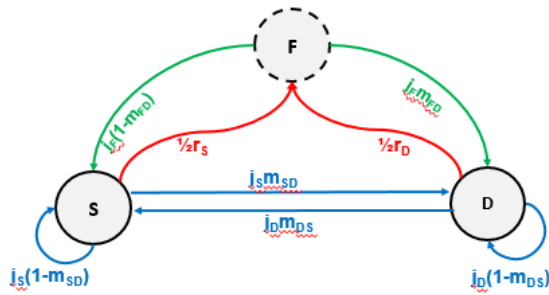
3

4 *Reproductive values as an integrated fitness measure*

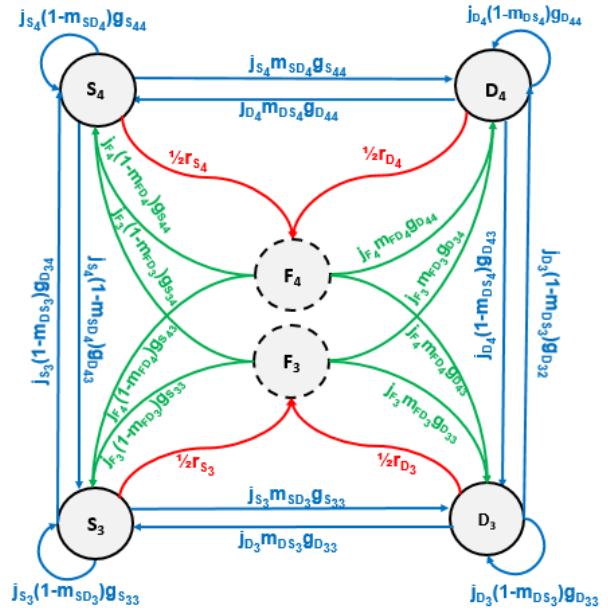
5 Fisher (1930) developed the concept of reproductive value in the context of his fundamental
6 theorem of natural selection to describe the expected contribution by individuals of a given age or
7 stage to future long-term growth of a population. A reproductive value approach uses age- or stage-
8 structured matrix models meaning that this fitness proxy is derived from explicit population
9 dynamic considerations. RV is thus a rate-sensitive fitness proxy that takes into account that the
10 timing of reproduction over a lifetime affects fitness in non-constant populations (Caswell 2001),
11 which is relevant as we study declining populations. Furthermore, RV is a model-based fitness
12 measure, meaning that it is amenable to formal sensitivity analyses developed in the field of
13 population matrix modelling (Caswell 2001), which allows us to determine the group size effects on
14 which fitness component are most important for overall fitness.

15 To determine the reproductive values of all group members in group-living species as function
16 of group size, one first constructs a life-cycle graph that describes the major life-stages and the
17 transition rates between them that represent the fitness components (reproduction, survival and state
18 change). In its simplest form the life-cycle of cooperative breeders can be described by three states
19 reflecting the social status of individuals (Fig. A1a): dominants, subordinates and fledglings (i.e.
20 offspring that leave ('fledge') the nest, but have not survived till the next year yet) and has the
21 following fitness components: number of fledglings produced (r) multiplied by probability that a
22 fledging survives until the next breeding season (j_F), the mean adult survival (j_S or j_D), as well as the
23 transition rates (conditional on survival) among states (m_{FD} , m_{SD} & m_{DS}), respectively the probability
24 that a fledgling, subordinate or dominant will be a dominant the next year. See Table A1 for an
25 overview of states, fitness components and abbreviations used in the paper.

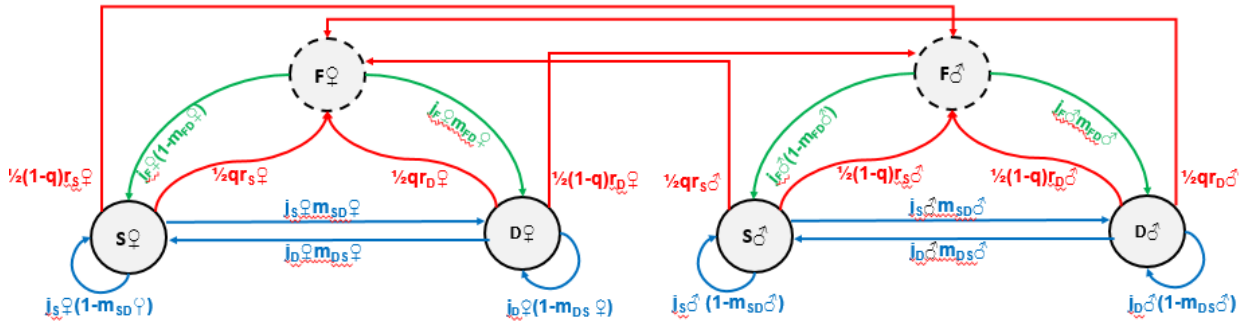
(a) Simplified life-cycle graph model of a group living species that ignores sex-differences and variation in group composition



(c) Simplified life-cycle graph model of a group living species that can live in groups of size 3 or 4, but ignores sex-differences



(b) Simplified life-cycle graph model of a group living species that includes sex-differences, but ignores variation in group composition



26

27

28 **Figure A1.** Simplified versions of the life-cycle graph used to model the effect of group size on the
 29 reproductive values of individuals of different sex and status, in different group sizes. a.) Arrows
 30 indicate the transition probabilities among states (Subordinates, Dominants and Fledglings)
 31 determined by the six fitness components: number of fledglings produced (r); probability of surviving
 32 till next breeding season for fledglings (j_F); the annual adult survival for subordinates and dominants
 33 (j_S & j_D); the transition rates (conditional on survival) among states (m_{FD} , m_{SD} & m_{DS}), the probability
 34 that a fledgling, subordinate or dominant respectively will be a dominant the next year. b.) This life-
 35 cycle can be extended to model two sexes and the transition probability among sexes governed by the
 36 offspring sex ratio (q). c.) This life-cycle can be further extended to model the transition probability

37 to move from a certain group size to another (g_F , g_S & g_D , in this example between group size 3 and
 38 4). Contributions to the next year's population via different fitness component are shown in different
 39 colours (reproduction in red, juvenile survival and recruitment in green, adult survival and state
 40 change in blue). Note that the dashed circle around the fledglings denotes that this state is not
 41 explicitly tracked in the model as we use a pre-breeding census model.

42

43 **Table A1.** Overview of the states and fitness components with their abbreviations used in our model
 44 (see Fig. A1).

Dimensions of state	Types and abbreviations
Social status	<u>F</u> ledgling, <u>S</u> ubordinate or <u>D</u> ominant
Sex	♀ or ♂
Group size	2,3,4,5,6+
Fitness components	Abbreviation
Group productivity (annual no. of fledglings produced per group)	h
Probability of within-group parentage	w
Number of extra-group fledglings	e
Annual survival probability	j
Probability of being dominant next year	m
Transition probability from group size in year t to year t+1	g

45

46 The basic life-cycle model depicted in Fig. A1a can be translated into the following matrix population
 47 model (Caswell 2001):

$$48 \begin{pmatrix} n_S \\ n_D \end{pmatrix}_{t+1} = \begin{pmatrix} \frac{1}{2}r_S j_F(1 - m_{FD}) + j_S(1 - m_{SD}) & \frac{1}{2}r_D j_F(1 - m_{FD}) + j_D m_{DS} \\ \frac{1}{2}r_S j_F m_{FD} + j_S m_{SD} & \frac{1}{2}r_D j_F m_{FD} + j_D(1 - m_{DS}) \end{pmatrix} \begin{pmatrix} n_S \\ n_D \end{pmatrix}_t \quad (\text{eq. 1})$$

49 With r being the annual number of fledglings in a given year. Eq 1 can be written more shortly as:

50 $\begin{pmatrix} n_S \\ n_D \end{pmatrix}_{t+1} = A \begin{pmatrix} n_S \\ n_D \end{pmatrix}_t = (R \circ J + K) \begin{pmatrix} n_S \\ n_D \end{pmatrix}_t$ (eq. 2)

51 $R = \begin{pmatrix} \frac{1}{2}r_S & \frac{1}{2}r_D \\ \frac{1}{2}r_S & \frac{1}{2}r_D \end{pmatrix}; J = \begin{pmatrix} j_F(1 - m_{FD}) & j_F(1 - m_{FD}) \\ j_F m_{FD} & j_F m_{FD} \end{pmatrix}; K = \begin{pmatrix} j_S(1 - m_{SD}) & j_D m_{DS} \\ j_S m_{SD} & j_D(1 - m_{DS}) \end{pmatrix}$

52 With R describing the matrix with the reproduction fitness component,

53 J describing the matrix with the juvenile survival and recruitment fitness components and K

54 describing the matrix with the adult survival and state change transition rates (the symbol \circ in eq. 2

55 implies the Hadamard product used in matrix algebra).

56 In order to provide intuitive insights into the interpretation of RVs and how they differ from

57 more conventional fitness measures, we can derive the RV (v in equations) for a constant population

58 in stable stage distribution (RVs used in the Results were calculated in a different way that does not

59 assume constant population size, see later). In such a situation, the reproductive values can be

60 analytically derived from the projection matrix A shown in equation 2 by solving $\mathbf{v}^T = \mathbf{v}^T A$ (e.g. Taylor

61 1990). For example the reproductive value of a dominant is:

62 $v_D = \frac{1}{2}r_D j_F ((1 - m_{FD})v_S + m_{FD}v_D) + j_D ((1 - m_{DS})v_D + m_{DS}v_S)$ (eq. 3)

63 This equation for the reproductive value has an intuitive interpretation: it is the sum of the current

64 reproductive value (first term) and the future (residual) reproductive value of an individual (second

65 term). The current reproductive values equals the number of offspring produced that survives till

66 adulthood $\frac{1}{2}r_D j_F$ (discounted by a half for sexually reproducing species) multiplied with the

67 reproductive value of a subordinate or dominant, depending on the probability of the offspring

68 acquiring subordinate or dominant status the next year $((1 - m_{FD})v_S + m_{FD}v_D)$. The future

69 reproductive values equals the survival of the adult (j_D) multiplied with the reproductive value of a

70 subordinate or dominant, depending on the probability the adult remains or loses dominance status

71 the next year $((1 - m_{DS})v_D + m_{DS}v_S)$.

72 It should be noted that this discounting, or weighting of the contribution of yourself and your

73 offspring to the next generation is an important feature of RVs that distinguishes it from simpler

74 fitness metrics popular among empiricists such as those that quantify fitness as (half) the number of

75 offspring produced plus your own survival. The reason this discounting is important is that for species
76 such as cooperative breeders, with a strong (st)age structure in reproduction and survival, the
77 contribution of certain type of individuals to the next generation can differ strongly (e.g. surviving
78 breeders are worth more—have a higher residual reproductive value—than an offspring that survives
79 to become a subordinate non-breeder; see also Fig. 4k&l).

80

81 *Adding sex-differences and variation in group composition*

82 The simplified life-cycle graph model in Fig. A1a can be expanded to include sex-differences and
83 sexual reproduction (Fig. A1b) and to include variation in group size (Fig. A1c). Sex differences are
84 straightforwardly included by defining all states to be sex-specific (female dominant, male dominant,
85 etc.) and by including a parameter q , reflecting the offspring sex ratio, that determines the probability
86 an individual will become female. We first illustrate the extension of the life-cycle model with group
87 size variation with an example for a cooperative breeder that can live in a group with either 3 or 4
88 members (1 to 2 subordinates and 2 dominant breeders). However, we later expanded this to cover
89 the full range of group sizes 2-6 and sex differences in one final model.

90 The life-cycle graph of Fig. A1c can be translated into the following matrix population model:

$$91 \begin{pmatrix} n_{S_3} \\ n_{D_3} \\ n_{S_4} \\ n_{D_4} \end{pmatrix}_{t+1} = \begin{pmatrix} \frac{1}{2}r_{S_3}j_{F_3}(1-m_{FD_3})g_{F_{33}} + j_{S_3}(1-m_{SD_3})g_{S_{33}} & \frac{1}{2}r_{D_3}j_{F_3}(1-m_{FD_3})g_{F_{33}} + j_{D_3}m_{DS_3}g_{S_{33}} & \frac{1}{2}r_{S_4}j_{F_4}(1-m_{FD_4})g_{F_{43}} + j_{S_4}(1-m_{SD_4})g_{S_{43}} & \frac{1}{2}r_{D_4}j_{F_4}(1-m_{FD_4})g_{F_{43}} + j_{D_4}m_{DS_4}g_{S_{43}} \\ \frac{1}{2}r_{S_3}j_{F_3}m_{FD_3}g_{F_{33}} + j_{S_3}m_{SD_3}g_{D_{33}} & \frac{1}{2}r_{D_3}j_{F_3}m_{FD_3}g_{F_{33}} + j_{D_3}(1-m_{DS_3})g_{D_{33}} & \frac{1}{2}r_{S_4}j_{F_4}m_{FD_4}g_{F_{43}} + j_{S_4}m_{SD_4}g_{D_{43}} & \frac{1}{2}r_{D_4}j_{F_4}m_{FD_4}g_{F_{43}} + j_{D_4}(1-m_{DS_4})g_{D_{43}} \\ \frac{1}{2}r_{S_3}j_{F_3}(1-m_{FD_3})g_{F_{34}} + j_{S_3}(1-m_{SD_3})g_{S_{34}} & \frac{1}{2}r_{D_3}j_{F_3}(1-m_{FD_3})g_{F_{34}} + j_{D_3}m_{DS_3}g_{S_{34}} & \frac{1}{2}r_{S_4}j_{F_4}(1-m_{FD_4})g_{F_{44}} + j_{S_4}(1-m_{SD_4})g_{S_{44}} & \frac{1}{2}r_{D_4}j_{F_4}(1-m_{FD_4})g_{F_{44}} + j_{D_4}m_{DS_4}g_{S_{44}} \\ \frac{1}{2}r_{S_3}j_{F_3}m_{FD_3}g_{F_{34}} + j_{S_3}m_{SD_3}g_{D_{34}} & \frac{1}{2}r_{D_3}j_{F_3}m_{FD_3}g_{F_{34}} + j_{D_3}(1-m_{DS_3})g_{D_{34}} & \frac{1}{2}r_{S_4}j_{F_4}m_{FD_4}g_{F_{44}} + j_{S_4}m_{SD_4}g_{D_{44}} & \frac{1}{2}r_{D_4}j_{F_4}m_{FD_4}g_{F_{44}} + j_{D_4}(1-m_{DS_4})g_{D_{44}} \end{pmatrix} \begin{pmatrix} n_{S_3} \\ n_{D_3} \\ n_{S_4} \\ n_{D_4} \end{pmatrix}_t$$

93 (eq. 4)

94 The subscript 3 and 4 refer to the number of subordinates in the group an individual lives in and $g_{D_{34}}$ is the probability a dominant in a group with one
 95 subordinate will be in a group with two subordinates the next year.

96 We can write this more shortly as:

$$97 \begin{pmatrix} n_{H_3} \\ n_{H_4} \end{pmatrix}_{t+1} = \begin{pmatrix} R_3^\circ J g_{F_{33}} + K_3^\circ G_{33} & R_4^\circ J g_{F_{43}} + K_4^\circ G_{43} \\ R_3^\circ J g_{F_{34}} + K_3^\circ G_{34} & R_4^\circ J g_{F_{44}} + K_4^\circ G_{44} \end{pmatrix} \begin{pmatrix} n_{H_3} \\ n_{H_4} \end{pmatrix}_t \text{ (eq. 5)}$$

$$98 G_{33} = \begin{pmatrix} g_{S_{33}} & g_{D_{33}} \\ g_{S_{33}} & g_{D_{33}} \end{pmatrix}; n_{H_3} = \begin{pmatrix} n_{S_3} \\ n_{D_3} \end{pmatrix}$$

99 **How promiscuity influences group size effects on fitness.**

100 Many organisms are genetically promiscuous despite forming socially monogamous pair bonds.
 101 Fairy-wrens are a prime example of this as they have among the highest rates of extra-pair and extra-
 102 group (with males from other groups) paternity recorded among birds (Cockburn et al. 2013).
 103 Promiscuity influences fitness calculations as the extra-group offspring of males are not reared in the
 104 group in which the male lives, and consequently some of their fitness components (e.g. juvenile
 105 survival and recruitment probability) do not depend on the group size of the father but on the group
 106 size where these extra-group offspring are reared. This complexity can be included by splitting the
 107 reproduction fitness component up into a component due to within- and extra-group parentage:

$$108 \quad R = \begin{pmatrix} \frac{1}{2}r_S & \frac{1}{2}r_D \\ \frac{1}{2}r_S & \frac{1}{2}r_D \end{pmatrix} = \begin{pmatrix} \frac{1}{2}(w_S h + e_S) & \frac{1}{2}(w_D h + e_D) \\ \frac{1}{2}(w_S h + e_S) & \frac{1}{2}(w_D h + e_D) \end{pmatrix} = \begin{pmatrix} \frac{1}{2}w_S h & \frac{1}{2}w_D h \\ \frac{1}{2}w_S h & \frac{1}{2}w_D h \end{pmatrix} + \begin{pmatrix} \frac{1}{2}p_S & \frac{1}{2}p_D \\ \frac{1}{2}p_S & \frac{1}{2}p_D \end{pmatrix} = W + E \text{ (eq. 6)}$$

109 With w_S being the probability of a subordinate being the genetic parent of an offspring in its own
 110 group (within-group parentage: it should be noted that in both SFW and RFW male subordinates
 111 sometimes have within-group paternity and that in RFW female subordinates can have within-
 112 group maternity if they build their own nest (plural breeding, Brouwer et al. 2011)). Furthermore, h
 113 is the number of fledglings per year reared in one's own group and p_D is the number of extra-group
 114 fledglings a dominant has sired (only males have extra-group parentage in both fairy-wren species).
 115 We can include the separation of within- and extra-group offspring and their different dependency on
 116 group size into the matrix model as follows:

$$117 \quad \begin{pmatrix} n_{H_3} \\ n_{H_4} \end{pmatrix}_{t+1} = \begin{pmatrix} W_3 \circ J_3 g_{F_{33}} + E_3 \circ \sum_{X=3}^4 (l_X J_X \circ G_{F_X}) + K_3 \circ G_{33} & W_4 \circ J_4 g_{F_{43}} + E_4 \circ \sum_{X=3}^4 (l_X J_X \circ G_{F_X}) + K_4 \circ G_{43} \\ W_3 \circ J_3 g_{F_{34}} + E_3 \circ \sum_{X=3}^4 (l_X J_X \circ G_{F_X}) + K_3 \circ G_{34} & W_4 \circ J_4 g_{F_{44}} + E_4 \circ \sum_{X=3}^4 (l_X J_X \circ G_{F_X}) + K_4 \circ G_{44} \end{pmatrix} \begin{pmatrix} n_{H_3} \\ n_{H_4} \end{pmatrix}_t \text{ (eq. 7)}$$

118 With l_x being the probability a male has extra-group parentage in a group with X subordinates, J_X
 119 being the juvenile survival and recruitment matrix for extra-group offspring reared in group size X
 120 and G_{F_X} being the group size transition matrix for extra-group offspring reared in a given group size
 121 to live in group size X the next year. In our model we assumed the group size in which males sired
 122 extra-group offspring was independent of the males own group size. Consequently, l_x simplifies to

123 the frequency of group size X in the population and G_{F_X} to a matrix with the transition rate to group
124 size X in year $t+1$ independent of group size in year t .

125 The final model included both sex-differences and variation in group size varying from 2-6.
126 From this model we derived the reproductive values for all adult group members
127 ($v_{D\sigma_2}, v_{S\sigma_2}, v_{S\varphi_2}, v_{D\varphi_2}, v_{D\sigma_3}, etc.$), by calculating the left eigenvector corresponding to the dominant
128 eigenvalue of the population projection matrix A (Caswell 2001). These reproductive values were
129 subsequently used to calculate the reproductive values for offspring as well ($v_{F\sigma_2}, v_{F\varphi_2}, v_{F\sigma_3}, etc.$).
130 As reproductive values are relative measures of fitness we standardized them by setting $v_{D\varphi_2} = 1$,
131 meaning that all reproductive values are in units of $v_{D\varphi_2}$.

132 We note that in our model all fitness components are locally density dependent (i.e. group size
133 effects), but we were unable to include any global density regulation. We acknowledge that omitting
134 any global density regulation is a shortcoming of our model. However, it is not a trivial matter to
135 determine how density dependence acts (e.g. at which life-stage(s) on which fitness component(s)
136 and at which spatial scale), while the choice of where to include density regulation in our life-cycle
137 model may have rather specific implications (Mylius and Diekmann 1995; Pen and Weissing 2000).
138 Regrettably, we do not have a clear enough understanding yet on how this complex process acts in
139 these species, for example in SFW a deteriorating environment has led to a complex temporal pattern
140 in declines in group size and the number of groups in our study area that requires further study.

141

142 ***Uncertainty in reproductive values***

143 We performed bootstrap analyses to quantify the amount of uncertainty in the estimates of model-
144 derived reproductive values based on the uncertainty in the input fitness parameter estimates. Based
145 on the statistical models for analysing the effects of group size on each fitness component, we
146 generated random variables on the scale of the link function used for each analysis. For example, for
147 juvenile female survival of individuals born in a group with 0 subordinates we drew bootstrap-values
148 from a logit-normal random variable with mean β_0 and standard deviation equal to the standard error

149 of β_0 . The values of β_0 and $s.e.(\beta_0)$ were derived from the intercept estimate from the model
 150 $\text{logit}(j) \sim \text{intercept} + \text{status} * \text{sex} * \text{groupsize}$ in which juvenile, female and group size of 2 were the
 151 reference category. We similarly used a logit-logistic regression model for the fitness components w ,
 152 m and q , while we used a log-Poisson regression model for the fitness components h and e , and a
 153 multinomial model for the fitness component g . This approach assures that bootstrapped values are
 154 both bounded (e.g. between 0 and 1 for binary/binomial variables), and that the asymmetry in upward
 155 and downward standard errors associated with bounded variables is translated into the reproductive
 156 values as well. We drew 1,000 bootstrap values of each of the random-variable fitness components to
 157 calculate the reproductive values for each of these bootstrap sets. These in turn were used to derive
 158 the asymmetric confidence intervals around the median reproductive values across all 1,000 bootstrap
 159 sets.

160

161 **Table A2.** Overview of the shape (Q= quadratic, L= linear) and direction (positive or negative) of
 162 the association between the six fitness components and group size for superb/red-winged fairy-
 163 wrens derived from a GLMM with group size fitted as a linear or quadratic term. ‘ns’ means the
 164 association was not statistically significant. ‘.’ = not available. Note that a positive quadratic
 165 indicates a parabola that opens downward and a negative quadratic a parabola that opens upward.

	Group productivity	Within group parentage	Extra- group paternity	Survival	Recruitment	Group size transition
Group	-Q/ns
Dominant ♀	.	./ns	.	ns/ns	ns/ns	-Q/-Q
Dominant ♂	.	-L/-L	-Q/+Q	ns/ns	ns/ns	-Q/-Q
Subordinate ♀	.	./-Q	.	./ns	./ns	./+L
Subordinate ♂	.	-L/ns	ns/-Q	-Q/-L	+Q/-L	-Q/+L
Fledgling ♀	.	.	.	ns/ns	ns/ns	ns/+L
Fledgling ♂	.	.	.	-Q/ns	ns/ns	+L/+L

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182

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