

Habitat structure influences parent-offspring association in a social lizard

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Provisional

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2

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18 **Abstract**

19 Parental care emerges as a result of an increase in the extent of interaction between parents
20 and their offspring. These interactions can provide the foundation for the evolution of a range
21 of complex parental behaviors. Therefore, fundamental to understanding the evolution of
22 parental care is an understanding of the factors that promote this initial increase in parent-
23 offspring association. Here, we used large outdoor enclosures to test how the spatial structure
24 of high-quality habitat affects the occurrence of parent-offspring associations in a social
25 lizard (*Liopholis whitii*). We found that the extent of parent-offspring association was higher
26 when high-quality habitat was aggregated relative to when it was dispersed. This may be the
27 result of greater competitive exclusion of adults and offspring from high quality crevices sites
28 in the aggregated treatment compared to the dispersed treatment. Associating with parents
29 had significant benefits for offspring growth and body condition but there were no
30 concomitant effects on offspring survival. We did not find costs of parent-offspring
31 association for parents in terms of increased harassment and loss of body condition. We
32 discuss a number of potential mechanisms underlying these results. Regardless of
33 mechanisms, our results suggest that habitat structure may shape the extent of parent-
34 offspring association in *L. whitii*, and that highly aggregated habitats may set the stage for the
35 diversification of more complex forms of care observed across closely related species.

36 **Key Words:** Parental Care, Parent-Offspring Association, Habitat Structure, Lizard, Social
37 Complexity

38 **Introduction**

39 The evolution of parental care is associated with an increase in the level of social interactions
40 between parents and offspring (Clutton-Brock, 1991; Smiseth et al., 2012). The result is a
41 range of complex and diverse parental behaviors (e.g., parental provisioning, care after
42 nutritional dependence) which can have profound effects on offspring development and
43 fitness (Clutton-Brock, 1991; Uller, 2012; Klug and Bonsall, 2014). These characteristics
44 also make parental care a key point in the adaptive radiation of kin relationships and sociality
45 (Queller, 1994; Field and Brace, 2004). Thus, there is enormous interest in understanding the
46 factors responsible for the initial emergence and subsequent diversification of parental care.

47
48 The majority of research on the evolution of parental care has focussed on identifying the
49 benefits of parental investment for offspring fitness (reviewed in Clutton-Brock, 1991; Royle
50 et al., 2012). Such benefits may be necessary for parental care to be selected; however, the
51 emergence of parental care will be facilitated, first and foremost, when parents regularly
52 encounter and associate with their offspring (Lion and van Baalen, 2007). Therefore,
53 conditions that promote increased levels of association between parents and their offspring
54 will be central to facilitating the early emergence of parental care (Wilson 1975; Lion and
55 van Baalen, 2007; Davis et al., 2011; Klug et al., 2012). Habitat availability and quality are
56 particularly important in this context. For example, limited availability of suitable habitat can
57 encourage offspring to delay dispersal and remain within the parental home range (Hatchwell
58 and Komdeur, 2000; Covas and Griesser, 2007). If this carries little or no cost to the parents,
59 they may tolerate offspring, resulting in an increased level of parent-offspring association.
60 Where these environmental conditions are recurrent, parent-offspring associations can create
61 a novel selective environment from which more complex forms of parental care, such as
62 parental provisioning, can evolve (e.g., Wong et al., 2013). Indeed, theoretical models have
63 shown that once this initial increase in parent-offspring association emerges parental care can
64 rapidly diversify and increase in complexity (e.g., Gardner and Smiseth, 2011).

65
66 Species in which parent-offspring associations are facultative or temporary, such as those
67 exhibited by some insects, fish, amphibians and lizards, provide excellent opportunities for
68 establishing the conditions that promote the early evolution of parental care (Kölliker, 2007;
69 Falk et al., 2014). In lizards, post hatching parent-offspring associations have been
70 demonstrated in at least 60 species (Somma, 2003; While et al. 2014). In most cases these
71 associations are characterized by semi-independent offspring remaining within the parental
72 home range (While et al., 2014). While this level of parent-offspring association is
73 considerably simpler than in many other vertebrates, it is characteristic of what we would
74 expect in the early stages of the evolution of postnatal parental care. Thus, these taxa provide
75 an opportunity to study how selection on more complex forms of parental care initially arise,
76 by examining the factors that influence increased parent-offspring association and the costs
77 and benefits of this association for both parties.

78
79 Here we conduct an experimental test of how habitat structure influences parent-offspring
80 associations and the consequences of this for offspring growth and survival in a social lizard
81 species, *Liopholis whitii*. *Liopholis whitii* lives in family groups characterized by stable (often
82 life-long) male-female pair bonds and prolonged parent-offspring associations (Chapple and
83 Keogh 2005; 2006; While et al., 2009a). These prolonged associations involve offspring
84 delaying dispersal and parents tolerating offspring within their core home ranges, sometimes
85 for up to several years. This has two potential benefits to offspring. First, offspring that
86 associate with their parents may gain access to parental resources (i.e., food within a parent's
87 habitat) and hence benefit in terms of increased growth and/or condition (O'Connor and

88 Shine, 2004; but see Langkilde et al., 2007). Second, offspring may gain survival benefits
89 through protection from infanticide (Sinn et al., 2008). Tolerance of offspring within the
90 home range may, however, also have costs to adults. For example, parental body condition
91 may be reduced through sharing resources with their offspring. Parents may also suffer injury
92 and/or reduced body condition through increased harassment from hungry conspecifics.

93

94 We manipulated habitat structure by manipulating the distribution of available crevice sites.
95 Rock crevice and burrow sites are a key component of *L. whitii*'s ecology and it has been
96 suggested that the structure and availability of these sites is fundamental in determining the
97 extent of parent-offspring associations in *L. whitii* and related species (Duffield and Bull,
98 2002; While et al., 2009a). We created two experimental treatments which differed in the
99 spatial association of crevice sites, a dispersed crevice site treatment whereby available
100 crevice sites were dispersed evenly across the environment and an aggregated crevice site
101 treatment, where available crevice sites were clumped together in a central location. We
102 predicted that the incidence of parent-offspring associations would be lower when suitable
103 crevice sites were clumped, as clumping of high quality habitats should lead to more frequent
104 agonistic encounters over access to high quality habitats between adult lizards from different
105 pairs and thus result in higher costs (and hence a lower incidence) of parents tolerating
106 offspring within their home range and defending these offspring from conspecific aggression.

107

108 **Methods**

109 **Study species**

110 *Liopholis whitii* is a medium sized (75-100 mm snout-vent length (SVL)) viviparous skink
111 that occurs throughout south-eastern Australia, including Tasmania (Chapple, 2003; Wilson
112 and Swan, 2003). It occupies a broad range of habitats (including coastal heaths, grasslands,
113 woodlands and dry sclerophyll forests) and altitudes (0-1600 m) (Cogger, 2003; Chapple,
114 2003; Wilson and Swan, 2003). Typically, *L. whitii* are closely associated with complex
115 burrow systems under/around rocks and shrubs (Chapple, 2003; Wilson and Swan, 2003)
116 where they typically focus their basking and foraging activities (Greer, 1989). Morphological
117 and life history traits vary geographically in *L. whitii* (Chapple, 2005). Tasmanian
118 populations are sexually monomorphic, mature at approximately three years and have a
119 lifespan of 9-10 years (While et al., 2009b). Reproduction occurs annually, with breeding
120 occurring in the austral spring (September-October) and gestation lasting 3-4 months (While
121 et al., 2007). Parturition occurs in the austral summer (January-February) with litters
122 comprising one to four offspring (most frequently two) born asynchronously, usually over
123 several days (While et al., 2007).

124

125 **Experimental Protocol**

126 We caught 160 *L. whitii* (80 males, 80 females) sourced from populations on the east coast of
127 Tasmania (approximately 42°57' S, 147°88' E) at the start of the breeding season (September
128 2013). Once captured, animals were transported in cool, damp cloth bags back to the
129 University of Tasmania (approximately an hour drive from the populations). At the
130 University, lizards were weighed (± 1 mg), measured for SVL and total length (± 0.5 mm),
131 indications of previous tail loss recorded, and gender determined via eversion of hemipenes.
132 Each lizard was uniquely toe-clipped to enable individual identification. Lizards were then
133 housed individually in plastic terraria (30 x 60 x 40 cm) kept under a 25 W basking light set
134 to an 8:16 hour light/dark cycle with overhead lights set on a 10:14 hour light/dark cycle.
135 Each terrarium had a basking rock underneath the basking light, with a wooden shelter at the
136 opposite end of the shelter. Lizards were provided with water and food (*Tenebrio* larvae and
137 fruit puree mixed with protein powder) *ad libitum*. Lizards were then moved to our large

138 enclosure facilities at the University of Tasmania's Cambridge Farm facility (16 enclosures,
139 each measuring 8 x 8 m) and assigned to one of two experimental treatments (eight
140 enclosures per experimental treatment).

141
142 The enclosures consisted of eight replicates for each of two treatments: 1; a dispersed crevice
143 site treatment, and 2; an aggregated crevice site treatment. The crevice sites within the
144 enclosures were constructed from either a wooden pallet, six hollow concrete bricks (Besser
145 blocks) and sand (representing high quality habitat) or two Besser blocks only (representing
146 low quality habitat). Each treatment had five of these high quality crevice sites and four low
147 quality crevice sites, but the arrangement of crevice sites between treatments differed, with
148 the high quality crevice sites spread apart in the dispersed treatment and aggregated together
149 in the center of enclosure in the aggregated treatment (Figure 1, Supplementary figure 1).
150 Enclosure treatments were paired, with the order of treatments randomized within each pair.
151 All enclosures were covered by bird netting to prevent predation by birds. While this removes
152 potential sources of mortality for both adult and offspring it is unlikely to influence the costs
153 and benefits of parent-offspring association themselves. Parent-offspring associations are
154 unlikely to function in a predator protection context, given that the majority of predators are
155 significantly larger than an adult *L. whitii* (e.g. include feral cats, snakes and large birds such
156 as kookaburras and ravens). Indeed, the main source of mortality for offspring and
157 harassment for parents is conspecifics (Lanham and Bull, 2000; O'Connor and Shine 2006).
158 The enclosures were stocked with water containers and live insects throughout the duration of
159 the experiment, with these resources distributed evenly throughout the enclosures.

160
161 Lizards were introduced into enclosures in October 2013. Five females and five males were
162 randomly assigned to each enclosure. This represented a similar, albeit slightly higher,
163 density to that found in natural populations (G. M. While pers. observation). This also
164 resulted in a match between the number of male/female pairs and number of high quality
165 crevice sites in each enclosure. Hence, the treatments differed only in the layout of the high
166 quality crevice sites, which were expected to be preferentially occupied by male/female pairs.
167 Lizards were semi-permanently marked with numbered cloth tape (Tesa, Hamburg,
168 Germany) to enable identification through observation of individuals. From October to
169 December 2013, the lizards were observed up to twice daily, once in the early morning and
170 once in the afternoon, by one experimenter (BH). These time periods were chosen to
171 correspond with the time when lizards are most active and do the majority of their basking
172 before seeking shelter in the middle of the day. The order of observations was rotated so that
173 the starting enclosure differed each observation session, while the order of enclosures
174 observed was consistent. Due to the weather dependence of lizard activity it was not always
175 possible to record observations at set times and in these instances observations were taken
176 opportunistically during the day whenever the weather permitted activity. During observation
177 session, data were collected on the locations of lizards in each enclosure and additional data
178 were taken on any observed interactions between lizards (such as fights or copulations).
179 Observations were made at least one meter from each enclosure to avoid disturbing lizards,
180 and an observation session ended when all enclosures had been thoroughly observed
181 (typically taking 10 minutes per enclosure) or when the lizards' activity period finished (i.e.,
182 when the weather became too hot or cold). If two observation sessions were taken on the
183 same the day, they were taken at least four hours apart to reduce spatial autocorrelation of
184 individual locations. In total we collected 2,874 observations.

185
186 At the start of January 2014 (i.e., at the end of gestation) individuals were captured from the
187 enclosures, brought back to the University, and housed as described above. Upon return to

188 the laboratory individuals were measured for the same traits taken at the start of the breeding
189 season (see above). Female terraria were checked daily for the birth of offspring. Upon birth,
190 the date of birth was recorded and offspring weight (± 1 mg (SE)), SVL (± 0.5 mm) and total
191 length (± 0.5 mm) were measured. Each juvenile was then given a unique toe-clip for
192 identification purposes. In total 67 females were recaptured in January, 37 of which gave
193 birth. This represents 55% of the female population reproducing, which is equivalent to that
194 observed in the natural population where only 68% of females give birth in a given year
195 (While et al. 2009; see also Chapple 2003 for the consistency of this pattern across *Egernia*
196 species). Before release, offspring were marked with a colored bee tag attached with non-
197 toxic glue (Pender Beekeeping Supplies), with five different colors corresponding to a
198 particular mother (Supplementary figure 2). Position of the tag along the offspring's back
199 identified which member of a litter it was (on the neck = 1st born offspring, on middle of the
200 back = 2nd born offspring, on the pelvis = 3rd born offspring; no litters contained more than
201 three offspring).

202

203 All individuals were then re-released into the enclosures from early to late February 2014. All
204 individuals were released at the crevice site within the enclosure that they were most
205 frequently observed (based on the 2,874 observational data points; see above). Offspring
206 were released with their mother at their mother's main crevice site. Daily observations were
207 then conducted by two experimenters (TBJ and EB) across both treatments following the
208 same protocols described for the October-December 2013 period. This resulted in a total of
209 4,235 independent observations for all individuals combined over 85 observational sessions.

210

211 Lizards were recaptured from late April to early May 2014, and brought back to the
212 University. On average, parents and offspring were in the enclosures for 58.75 ± 0.52 days.
213 The adults were measured for weight (± 1 mg), SVL (± 0.5 mm), total length (± 0.5 mm), toe
214 and tail loss. The juveniles were measured for weight (± 1 mg), SVL (± 0.5 mm), total length
215 (± 0.5 mm) and tail loss. All individuals were then released back into the natural populations
216 from which they came.

217

218 **Parentage Assignment**

219 All individuals included in the study were genotyped for six microsatellite loci (EST1, EST2,
220 EST4, EST12: Gardner et al., 1999; TruL12, TruL28: Gardner et al., 2008) using standard
221 molecular techniques with DNA extracted from tail tip samples (see While et al., 2009a, b for
222 further details). Paternity was assigned using the computer program CERVUS 3.0 (Marshall
223 et al., 1998) using the following simulation parameters: 10,000 cycles, 95 % of candidate
224 parents sampled, 85 % loci typed and a genotyping error rate of 1 % (calculated in CERVUS
225 from our data). The one known parent option was used with all adult males released into the
226 same enclosure as the mother included as possible fathers. Paternity was assigned to the male
227 with the highest male-female-offspring trio LOD score and the lowest number of mismatches
228 (0 or 1) (e.g., Foerster and Kempnaers, 2004; Chapple and Keogh, 2005). Because there
229 were only five possible fathers for any offspring within an enclosure, paternity could be
230 assigned with high confidence in the majority (>90 %) of cases. Seven out of 76 offspring
231 could not be confidently assigned paternity (had ≥ 2 loci mismatches) and were thus excluded
232 from analyses of father-offspring association.

233

234 **Home range analysis and assignment of parent-offspring associations**

235 Parent home ranges were constructed using the program ArcView3.3 (ESRI) using a fixed
236 kernel analysis with a least squares cross-validation smoothing parameter (Powell, 2000).

237 Core home range was calculated using 50 % isopleths. For *L. whitii* and related species, this

238 area represents an individual's permanent shelter site from which it basks, feeds and
239 undertakes the majority of its social behavior (e.g., While et al., 2009a). Adults with less than
240 eight observations were excluded from the analysis ($n = 20$) as home ranges could not be
241 constructed for these individuals. The low number of average sightings of juveniles relative
242 to adults (juveniles = 8 ± 1 , adults = 25 ± 1) prevented the assignment of presence or absence
243 of parent-offspring association based on parent-offspring home range overlap. Instead, based
244 on long-term monitoring of a wild population for which home range overlap is available
245 (While et al. 2009a,b) we defined a parent-offspring association when juveniles had 50% or
246 more of their observations within their parent's core home range area (see also While et al.,
247 2009a, b). The average percentage of observations for offspring assigned as being associated
248 with their parents was $73 \pm 5\%$ and $72 \pm 9\%$ for mothers and fathers respectively compared
249 to $8 \pm 2\%$ and $3 \pm 1\%$ for offspring who were not associated with their parents.

250

251 **Data analyses**

252 Data were analyzed using General and Generalized Linear Mixed Models fitted using
253 maximum likelihood implemented in R version 3.0.2 (R development core team 2014), using
254 either the 'glmer' (for binary response variables) or 'lmer' function (for continuous response
255 variables) under the 'lme4' package (Bates et al., 2012). All models used the Laplace
256 approximation to estimate model parameters, as it is considered a more accurate technique
257 than the simpler pseudo quasi-likelihood estimation method (Bolker et al., 2009). Models
258 regarding offspring traits included parental ID as a random factor to account for non-
259 independence arising from litters containing multiple offspring. All models also included
260 enclosure as a random factor to account for differences between enclosures. Because of
261 limited sample size we ran main effects models only and models for maternal and paternal
262 parental-offspring association were run separately. The low incidence of bi-parental parental-
263 offspring association (only 2 cases total) precluded its analysis.

264

265 All fixed effects were tested with Wald's χ^2 and type III F tests (Kenward-Rogers
266 approximation for F tests) obtained with the 'car' package (Fox et al., 2014). All models were
267 checked for violation of assumptions. All results are reported as means, with standard errors
268 as the measure of variability.

269

270 *Parent-offspring association*

271 The effect of habitat structure on the extent of parent-offspring association was analyzed by
272 examining the proportion of parents whose offspring remained within their home range, using
273 a Generalized Linear Mixed Model with the binomial family specified. These models
274 included treatment (clumped vs. aggregated treatment) as a fixed factor, parental body
275 condition as a covariate, and enclosure as a random factor. Body condition (as an indicator of
276 an individual's energy stores relative to structural components of the body) was measured by
277 taking mass divided by SVL. This has been suggested as a reliable index of body condition
278 (Green, 2001; Labocha et al., 2014). Analyses of body condition excluded individuals who
279 had lost tails (as tail loss affects mass and therefore estimates of body condition). We then
280 examined the relative occurrence of parent-offspring associations on high versus low quality
281 habitats between treatments, and the extent to which adults and offspring occupied high
282 versus low quality habitats between treatments. We assigned individuals as occupying either
283 high or low quality habitat based on the location of their home ranges (for adults) or where
284 50 % or more of their observations occurred (for offspring). Individuals whose home range or
285 majority of observations occurred primarily on grass areas (i.e., neither pallets nor Besser
286 blocks) were excluded from analysis. These analyses were run using Generalized Linear
287 Mixed Model's with treatment as a fixed factor and enclosure as a random factor.

288 *Consequences of parent-offspring association for offspring*
289 Benefits of parent offspring association for offspring were analyzed in terms of skeletal
290 growth, body condition and survival. Change in SVL between the start and end of the
291 experiment was used to assess offspring skeletal growth (SVL is a common measure of
292 growth for reptiles – e.g., Shine and Charnov, 1992). Analysis of growth used a General
293 Linear Mixed Model with treatment (i.e., aggregated vs. dispersed habitat treatments) and
294 mother-offspring association as fixed factors, the number of days spent in an enclosure as a
295 covariate, and maternal and enclosure ID as random effects. The difference in offspring body
296 condition between treatments at the end of the experiment was analyzed using a Generalized
297 Linear Mixed Model with treatment and mother-offspring association as fixed factors, initial
298 offspring body condition and the number of days spent in an enclosure as covariates, and
299 maternal and enclosure ID as random effects. As there were only 3 cases where offspring
300 associated with their father and we had corresponding measurements for offspring growth
301 and body condition, we ran the above models for mother-offspring association only. Finally,
302 we analyzed differences in offspring survival by running a Generalized Linear Mixed Model
303 on the survival status of offspring (recaptured = survived, not recaptured = dead) at the end of
304 the experiment. These models had mother-offspring association (yes or no), father-offspring
305 association (yes or no) and treatment as fixed factors and parental and enclosure ID as
306 random effects.

307

308 *Consequences of parent-offspring association for parents*

309 Increased parent-offspring association may have a number of fitness costs for parents in
310 terms of decreased body condition associated with sharing resources with offspring and
311 increased harassment from other lizards. To test how marks of harassment varied between
312 parents who associated with their own offspring and those who did not and between the two
313 treatments, we used both tail and toe loss as a proxy (loss of tails and toes are key indicators
314 of intraspecific competition in lizards, especially where predation has been eliminated:
315 Norris, 1953; Tinkle, 1967; Vitt et al., 1974). Tail and toe loss were entered as a binary
316 response variable in four separate main effects models (one for each sex and each trait), with
317 parent-offspring association and treatment as fixed factors. Including enclosure ID as a
318 random factor resulted in poor model convergence and was excluded from these models. To
319 test consequences of parent-offspring associations for adult body condition, we ran a General
320 Linear Mixed Model with parent body condition at the end of the experiment as a response
321 variable, parent-offspring association and treatment as fixed factors, initial parental body
322 condition as a covariate, and enclosure I.D. as a random factor.

323

324 **Results**

325 Seventy six offspring were born in the laboratory to 37 mothers (average brood size = $2.05 \pm$
326 0.13) and released with their parents into the large outdoor enclosures. Thirty nine of the 76
327 offspring released into the enclosures were recaptured at the conclusion of the observation
328 sessions in April/May, representing an overall survival of 53 %. Survival of adults from
329 release at the start of February until April/May was high, at 95 %. Average adult home range
330 size during this period was the same between treatments (aggregated = $7.81 \pm 0.72\text{m}^2$,
331 dispersed = $6.42 \pm 1.05\text{m}^2$; $F_{1, 13.58} = 1.20$, $p = 0.29$) and between males and females (males =
332 $6.34 \pm 0.51\text{m}^2$, females = $7.89 \pm 1.20\text{m}^2$; $F_{1, 122.78} = 1.48$, $p = 0.23$). The extent to which low
333 versus high quality crevice sites were occupied by adults differed significantly between
334 treatments ($\chi^2 = 21.44$, $p < 0.01$). In the aggregated treatment 14 of the 39 adults who
335 occupied crevice sites occupied high quality sites (36 %) compared to 46 of the 54 adults
336 (85 %) in the dispersed treatment. For offspring in the aggregated treatment 6 of the 13
337 (46 %) offspring who occupied crevice sites occupied high quality sites compared to 5 out of

338 the 10 offspring (50 %) in the dispersed treatment ($\chi^2 = 1.00, p = 0.32$). The remaining adults
339 and offspring established themselves away from the crevice sites in grass patches or the
340 perimeter of the enclosure.

341

342 *Parent-offspring association*

343 Of the 37 females who produced offspring, there was sufficient observational data to
344 establish the extent of mother-offspring association for 34 mothers. Overall, 12 out of these
345 34 mothers (35 %) associated with their offspring. The extent of mother-offspring association
346 differed significantly between treatments (Table 1). Specifically, 9 out of 15 mothers (60 %)
347 associated with their offspring in the aggregated treatment compared to 3 out of 19 (16 %) in
348 the dispersed treatment. Of the 28 males who sired offspring, there was sufficient
349 observational data to establish the extent of father-offspring association for 25 fathers.
350 Overall, 7 of these 25 fathers (28 %) associated with their offspring; 5 out of 12 fathers
351 (43 %) in the aggregated treatment and 2 out of 13 (15 %) in the dispersed treatment. This
352 difference failed to reach statistical significance (Table 1). There was no effect of a mother's
353 or father's initial body condition on whether or not they associated with their offspring (Table
354 1). An analysis at the offspring level produced qualitatively similar results, with 35% and
355 19% of offspring in the aggregated treatment associating with their mother and father
356 respectively, compared to 9% and 10% in the dispersed treatment. However, these
357 differences were not statistically significant (Mother: $\chi^2 = 2.32, p = 0.13$; Father: $\chi^2 = 0.095, p$
358 $= 0.33$). The ratio of parent-offspring associations formed on low versus high quality crevice
359 sites was higher in the aggregated compared to the dispersed treatment. Only five out of 14
360 parent-offspring associations (36 %) in the aggregated treatment occurred on high quality
361 crevice sites, compared to 4 out of 5 (80 %) in the dispersed treatment. This difference,
362 however, was not significant ($\chi^2 = 0.95, p = 0.33$).

363

364 *Consequences of parent-offspring association for offspring*

365 Sixty nine percent (9/13) of offspring that associated with their mother survived, compared to
366 62 % (25/40) offspring that did not ($\chi^2 = 0.06, p = 0.81$). These results were mirrored in the
367 data collected on paternal-offspring association ($\chi^2 = 1.85, p = 0.17$). Specifically, 3 out of 7
368 (43 %) offspring that associated with their father survived, and 25 out of 40 (62 %) offspring
369 that did not associate with their father survived. Offspring survival did not differ between
370 treatments (aggregated treatment = 57 % (20/35), dispersed treatment = 43% (19/41); $\chi^2 =$
371 $1.03, p = 0.31$).

372

373 Mother-offspring association had a significant effect on offspring growth and body condition
374 (Table 2). Offspring that were associated with their mother had increased growth and were in
375 better body condition at the end of the experiment relative to those who were not (Figure 2a
376 and Figure 2b). There was no significant effect of treatment on either offspring SVL growth
377 or change in body condition (Table 2).

378

379 *Consequences of parent-offspring association for parents*

380 We found no costs of increased parent-offspring association for mothers or fathers in the
381 form of harassment suffered from conspecifics (e.g., frequency of tail and toe loss did not
382 differ between treatments for mothers or fathers; Table 3). There was no difference in mother
383 or father body condition at the end of the experiment between those parents who did and did
384 not associate with their offspring nor were there any differences between treatments (Table
385 3).

386

387

388 **Discussion**

389 Testing how the structure of the environment influences associations between offspring and
390 their parents is fundamental to our understanding of the origins of parental care (Gardner and
391 Smiseth, 2011; Klug et al., 2012). Here we show that approximately a third of males and
392 females associate with their offspring following birth. This level of parent-offspring
393 association is in accordance with what is observed in the wild, where the number of parents
394 associating with offspring can vary from between 10 – 70% (While et al. 2009b; Botterill-
395 James et al. unpublished data). We further show that the structure of high quality habitat
396 significantly influenced the extent of parent offspring association. This increased parent-
397 offspring association has benefits for offspring growth and body condition, but does not
398 appear to carry a substantial cost for parents. Below, we discuss our results in the context of
399 findings in other species, the mechanisms which may underlie the observed effects of habitat
400 structure on parent-offspring associations, and discuss the broader implications of these
401 findings for the evolutionary origins of more complex forms of parental care.

402

403 Habitat structure and availability is an important ecological variable in *Liopholis whitii*,
404 which has been suggested to influence the social complexity of this and other species of
405 *Egernia*. (Duffield and Bull, 2002; Chapple, 2003; O'Connor and Shine, 2003; While et al.,
406 2009a). Here we experimentally demonstrate that the spatial aggregation of high-quality
407 crevice sites promote parent-offspring association. Specifically, both mothers and fathers
408 were more likely to associate with their offspring when high quality habitat was aggregated
409 compared to when it was dispersed, although that latter result failed to reach statistical
410 significance. These results are consistent with the suggestion that the availability and
411 structure of habitat are key to facilitating the evolution of postnatal parental care by
412 increasing habitat sharing between closely related individuals (Wilson, 1975; Lion and van
413 Baalen 2007). This is believed to be fundamental to the formation of family groups across the
414 *Egernia* (Duffield and Bull, 2002; Chapple, 2003; O'Connor and Shine, 2003; While et al.,
415 2009a), but current empirical evidence for this hypothesis is mixed. For example,
416 manipulation of shelter availability in *E. striolata* altered adult pair bonding, with more pairs
417 forming when shelter availability was low (Lancaster et al., 2010), whereas Gardner et al.
418 (2007) found no effect of crevice site abundance on social group structure in *Egernia stokesii*.

419

420 Despite a general effect of habitat structure on parent-offspring association the direction of
421 this effect requires some explanation. Specifically, there was a greater level of parent-
422 offspring association when high-quality habitat was aggregated compared to when it was
423 dispersed. This is perhaps counter-intuitive; it might be expected that there would be strong
424 costs to parents from associating with offspring in the aggregated treatment, due to increased
425 harassment from conspecifics relative to the dispersed treatment. However, we found little
426 evidence that parental-offspring association carries costs to either parent. The analysis
427 looking at where adults and offspring settled within enclosures suggests an alternative
428 explanation. Adult, but not offspring, occupation of low versus high quality habitats differed
429 between treatments; more adults were present on low quality habitats in the aggregated
430 treatment, probably as a result of competitive exclusion from home ranges of dominant
431 individuals. There were also more parent-offspring associations formed on low versus high
432 quality habitats in the aggregated treatment (although the low statistical power limited the
433 confirmation that this deviated from the null expectation of no difference between habitats).
434 The tight spacing of crevice sites in the aggregated treatment may therefore have facilitated
435 their monopolization by a small proportion of adults while the majority of (more subordinate)
436 adults were forced into the lower quality areas. This would then increase habitat saturation
437 and reduce the overall availability of crevice sites (both of high and low quality) facilitating

438 greater overlap of habitat use between these adults and their offspring, with this overlap then
439 maintained by no/low costs of parent-offspring association for adults. Therefore, enhanced
440 parent-offspring association may be a result of some adults being restricted to low quality
441 habitats where the majority of offspring are residing as opposed to any benefits of delayed
442 dispersal to offspring *per se*. This supports natural population data on *E. saxatilis*, where
443 habitats occupied by solitary versus parentally-associated offspring were similar when
444 measured across a range of habitat quality indicators (Langkilde et al., 2007). Further tests
445 are required to confirm whether the proposed explanation of habitat monopolization (and
446 forced habitat sharing between ousted parents and their offspring) is the mechanism
447 responsible for the observed pattern of parent-offspring association. This could be achieved
448 by directly manipulating habitat density rather than structure or by altering dominance-
449 subordination hierarchies within enclosures (similar manipulations have been performed, for
450 example, to examine the evolution of sociality in coral fish – Buston, 2004). Additionally,
451 this mechanism could be investigated by observing natural populations and determining the
452 frequency of parent-offspring associations across environments that differ in density (and
453 hence availability) of suitable habitats, and determining whether less dominant individuals
454 (assessed by behavioral interactions or their location on lower quality crevice sites) more
455 often associate with their offspring. These offer potential avenues for future research.

456
457 There were clear benefits for offspring that associated with their mother. Specifically,
458 offspring who resided within their mother’s home range grew significantly more and were in
459 significantly better body condition at the end of the experiment than offspring who did not.
460 There are at least two mechanisms that could lead to these benefits. First, parental protection
461 from conspecific harassment may allow offspring to spend more time foraging freely. Such
462 an effect has been demonstrated in the laboratory for the related *Egernia saxatilis* (O’Connor
463 and Shine, 2004). Second, offspring growth could simply result from a higher resource
464 availability within their parent’s relatively high quality habitat compared to what they would
465 encounter if they dispersed (Duffield and Bull, 2002). However, our results suggest no
466 ‘resource access’ benefits, as parent-offspring associations tended to form on low quality
467 habitat sites. Characterization of habitats occupied by offspring associated versus not
468 associated with their parents, and detailed observational studies that look at how parental
469 presence influences offspring foraging behavior are potential research directions to
470 consolidate our understanding in this system of the mechanisms underlying the positive effect
471 of mother-offspring association on offspring growth and body condition. Alternatively, the
472 increased offspring growth and body condition may be a result of parental effects as opposed
473 to benefits acquired as a result of association *per se*; however, we did not find that parents in
474 better body condition (as a proxy of parental quality) were more likely to associate with their
475 offspring.

476
477 Despite benefits of maternal association for offspring growth, we did not find any benefits for
478 survival. This was surprising given that one of the key hypotheses for the benefits of parent-
479 offspring association in the *Egernia* lineage of lizards is protection from conspecific
480 infanticide (Langkilde et al., 2007; Sinn et al., 2008). Our results instead suggest that parental
481 tolerance of offspring has the primary function of enabling a safer and more efficient foraging
482 environment, as opposed to direct protection from conspecifics. In support of this conclusion,
483 *L. whitii* and other species of *Egernia* have been shown to tolerate their own, but not
484 unrelated offspring, within their home range (O’Connor and Shine, 2004; While et al.,
485 2009a); if parental-offspring association has low costs, the presence of unrelated offspring
486 may nevertheless negatively affect a parent’s own offspring through competition over
487 resources within the parent’s habitat. The observation of parental aggression towards

488 unrelated offspring fits this ‘resources or foraging benefits’ hypothesis. If parental-offspring
489 association has benefits for protection from infanticide, we would expect no parental
490 aggression towards unrelated offspring, as this should not increase the risk of infanticide to
491 the parent’s genetic offspring (and may even reduce it, through a dilution effect).

492
493 We found no costs to parents of associating with offspring. This was true when costs were
494 measured both in terms of body condition or marks of aggression suffered. This is consistent
495 with studies on reptiles more broadly where the costs associated with the early stages of
496 parental care are often small (Aubret et al., 2005; Huang, 2007; Stahlschmidt et al., 2012). An
497 absence of costs associated with increased parent offspring association may help facilitate the
498 evolution of more complex forms of care because it promotes a kin structure that could favor
499 the expression of more costly behaviours (for example, parental provisioning). However,
500 similar to many other studies, the lack of costs to parents may be because true fitness costs
501 are difficult to detect from a single season analysis (reviewed in Alonso-Alvarez and
502 Velando, 2012) and with low sample size (Graves, 1991). Thus, more data on the long-term
503 consequences of increased parent-offspring association for both parents and offspring is
504 required.

505
506 This study has provided evidence for effects of habitat structure on the extent of parental-
507 offspring association within *L. whitii*. We believe that such a simple increase in parental-
508 offspring association may be characteristic of the early stages of the evolution of complex
509 forms of parental care and group living. When the costs to care are low, parents will tolerate
510 offspring, facilitating prolonged associations between parents and offspring. This enhanced
511 kin association sets the foundation from which more complex care behaviors can emerge. The
512 *Egernia* lineage show variation between populations and species in the environments they
513 inhabit and the degree to which they associate with offspring (from no care in species such as
514 *L. inornata*, to extended family groups with multiple cohorts of offspring cared for in *E.*
515 *cunninghami* – reviewed in Chapple, 2003; While et al. 2015). These species therefore offer
516 opportunities to connect within species patterns between ecology and parent-offspring
517 association with the emergence and diversification of more complex forms of parental care
518 across species in the *Egernia* lineage. Ultimately this will provide a greater understanding of
519 the casual effects of specific ecological conditions on the emergence of parental care more
520 broadly.

521

522

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753

754 **Table 1:** Output from models testing for differences in parent-offspring association in
755 *Liopholis whitii* between treatments and in relation to parental condition. Statistically
756 significant P-values are in bold.

Factor	Mother-Offspring		Father-Offspring	
	χ^2	p	χ^2	p
Treatment	4.58	0.03	3.57	0.06
Parental Condition	0.29	0.58	1.28	0.26

757
758

Provisional

759 **Table 2:** Output from models testing for effect of treatment and parent-offspring association
 760 on offspring growth and condition in *Liopholis whitii*. Statistically significant P-values are in
 761 bold.

Factor	Offspring SVL Growth		Offspring Condition	
	F	p	F	P
Treatment	$F_{1,7.42} = 0.01$	0.91	$F_{1,4.81} = 0.33$	0.59
Maternal Association	$F_{1,24.85} = 5.51$	0.03	$F_{1,12.14} = 9.16$	0.01
Days in Enclosure	$F_{1,24.17} = 24.17$	0.04	$F_{1,14.83} = 5.41$	0.03
Offspring Condition at Release			$F_{1,12.62} = 13.28$	0.003

762

Provisional

763 **Table 3:** Output from models testing for effect of treatment and parent-offspring association on parental condition and harassment in *Liopholis*
 764 *whitii*. Statistically significant P-values are in bold.
 765

Factor	Mother Toe Loss		Father Toe Loss		Mother Tail Loss		Father Tail Loss		Mother Condition		Father Condition	
	χ^2	p	χ^2	p	χ^2	p	χ^2	p	F	p	F	p
Treatment	0.02	0.89	1.62	0.20	0.23	0.63	0.05	0.82	$F_{1,15.02} = 1.77$	0.20	$F_{1,6.53} = 0.84$	0.39
Parental Association	0.43	0.51	1.62	0.20	0.82	0.37	0.92	0.34	$F_{1,19.73} = 3.58$	0.07	$F_{1,11.98} = 0.81$	0.38
Days in Enclosure	4.26	0.04	0.45	0.50	1.31	0.25	1.37	0.24	$F_{1,18.82} = 2.17$	0.16	$F_{1,9.97} = 0.02$	0.88
Condition at Release									$F_{1,13.96} = 7.02$	0.02	$F_{1,10.61} = 20.41$	<0.01

766

767 **Figure captions**

768

769 Figure 1: Diagrammatic representation of the two treatments used in the experiment. On the
770 left is the dispersed habitat treatment and on the right is the aggregated treatment. Areas
771 representing high quality and low quality habitat indicated.

772

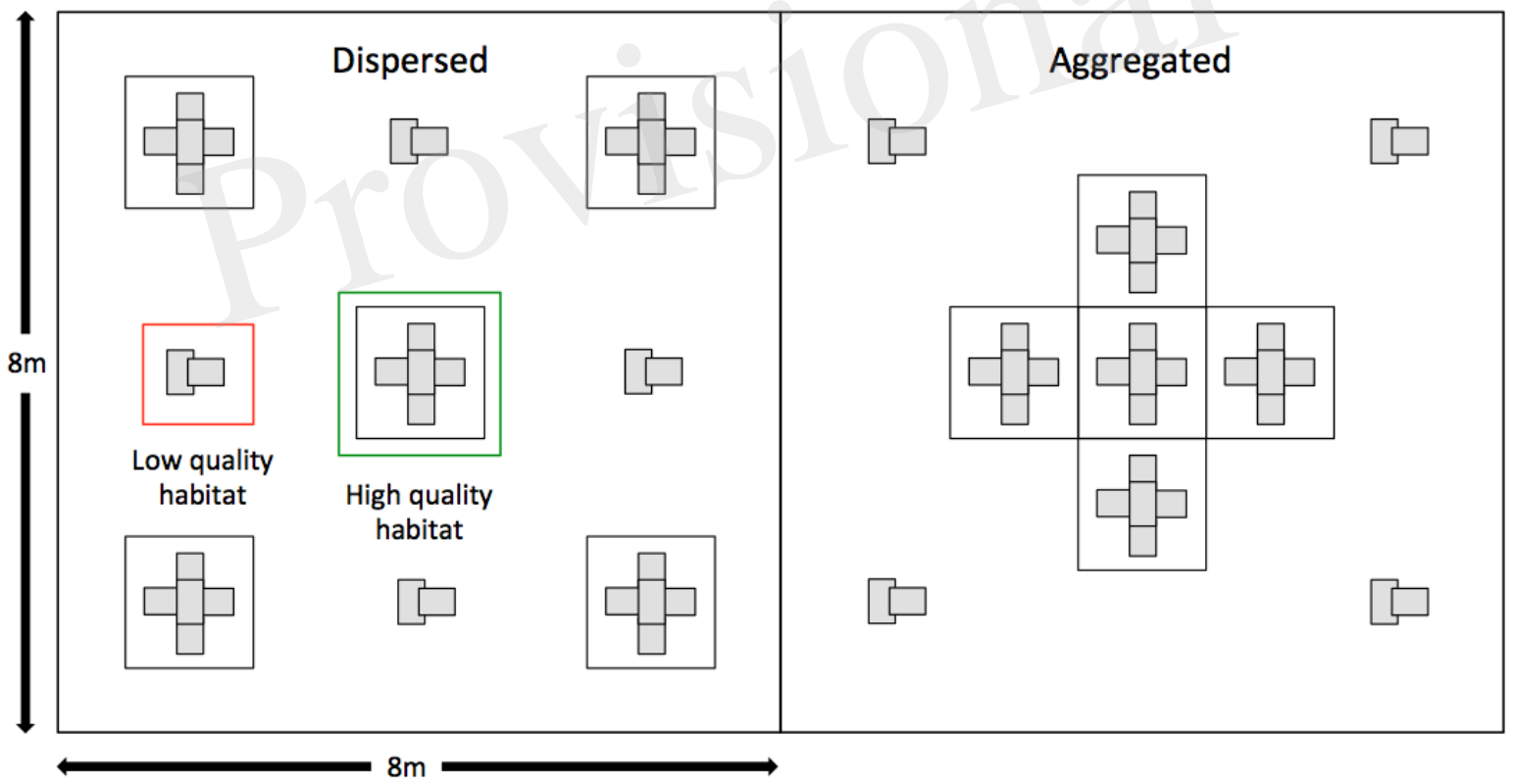
773 Figure 2: Difference in offspring svl growth (mm) (a) and offspring body condition (mg/mm)
774 (b) between offspring who associated with their mother and those who did not. Black data
775 points indicate offspring from the clumped treatment, grey data points indicate offspring from
776 the dispersed treatment.

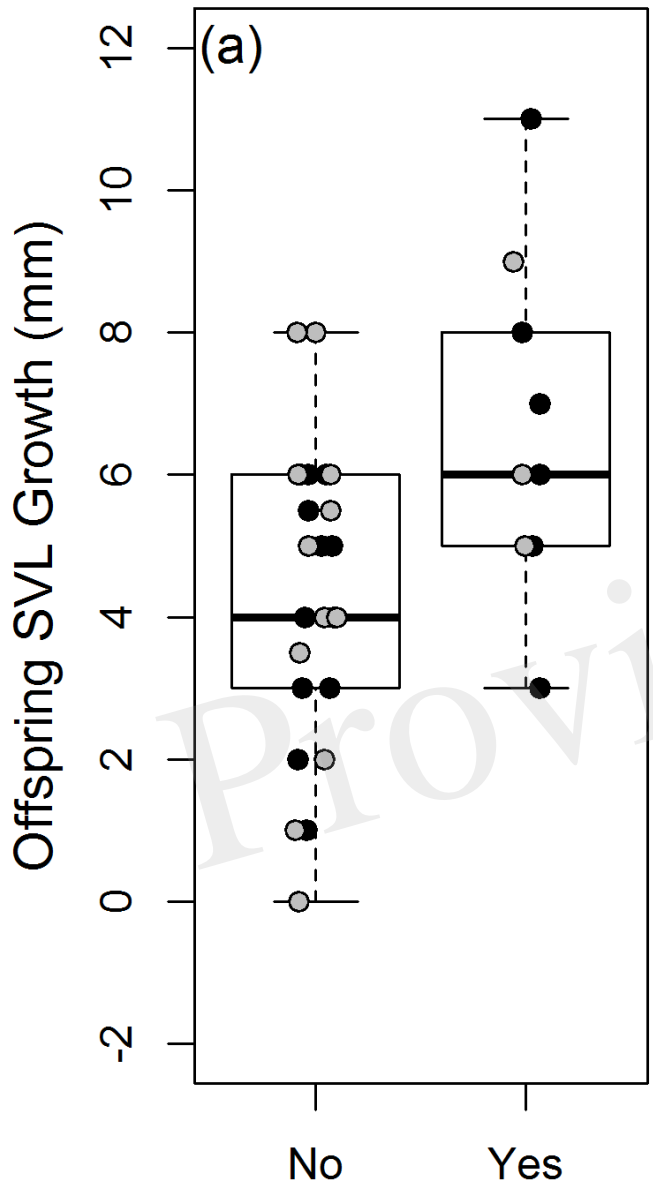
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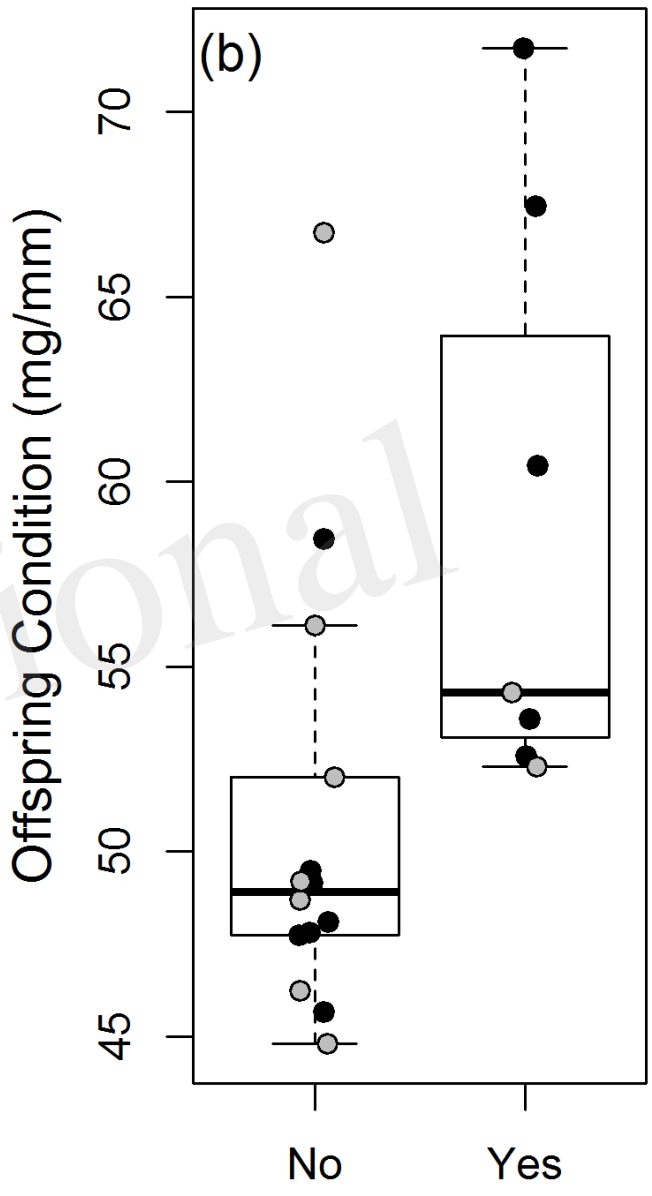
Provisional

Figure 01.TIFF





Mother-Offspring Association



Mother-Offspring Association