



Original Article

# Habitat saturation promotes delayed dispersal in a social reptile

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When and where offspring disperse has important implications for the evolutionary emergence and maintenance of group living. In noncooperative breeders, direct benefits of delayed dispersal are relatively limited, suggesting that decisions regarding whether or not to remain in the parental territory are largely driven by the availability of suitable habitat in which to settle. Although there is ample evidence of correlations between habitat saturation and delayed dispersal, experimental tests are rare, particularly for species with facultative group formation. We manipulated the density of conspecifics in enclosed populations of a family living reptile to experimentally evaluate the influence of habitat saturation on the tendency to delay dispersal. Habitat saturation did not influence whether or not offspring explored their surroundings. However, when conspecific density was high, more offspring delayed dispersal and those that did settle in high-density enclosures had reduced survival. These patterns appear to be due to increased dispersal costs imposed by conspecific aggression; offspring that explored high-density enclosures had reduced body condition and a greater risk of mortality. We discuss these results in the context of the evolutionary origins of family living.

**Key words:** dispersal, *Egernia*, habitat saturation, philopatry, social organisation.

## INTRODUCTION

When and where to disperse are decisions faced by offspring that have significant implications for the size and stability of family groups and ultimately the opportunity for selection on cooperative behavior between kin (Spinks et al. 2000; Le Galliard et al. 2003; Lucia et al. 2008). Indeed, delayed dispersal and cooperation represent a fundamental co-evolutionary feedback in the emergence and elaboration of complex social systems (Le Galliard et al. 2005a). A crucial step in understanding the origin and maintenance of group living is therefore to understand factors that mediate offspring dispersal.

Dispersal decisions are shaped by the costs and benefits of dispersal and philopatry. Dispersing is often crucial to avoid competition with kin (Hamilton and May 1977), but it also carries costs. In particular, if settlement is limited by extrinsic

factors, such as a shortage of suitable habitat (Komdeur 1992; Walters et al. 1992), a shortage of mates (Pruett-Jones and Lewis 1990), a low probability of successful independent breeding (Emlen 1982; Stacey and Ligon 1987), or enhanced mortality of dispersers (Heg et al. 2004; Bach et al. 2006). Dispersal entails additional costs when offspring forfeit benefits associated with philopatry, including nepotistic access to resources (Ekman and Griesser 2002; Dickinson and McGowan 2005), protection from conspecific aggression (Black and Owen 1987; O'Connor and Shine 2004), or predation (Griesser and Ekman 2005; Griesser et al. 2006), and the inheritance of parental territories (Ekman et al. 2001; Kokko and Ekman 2002). Recent research suggests that benefits, constraints and particular life history characteristics act in concert to bias the cost-benefit trade-off of dispersal and create demographic conditions conducive to philopatry (Covas and Griesser 2007; Hatchwell 2009). Indeed, the selection dynamics surrounding dispersal are often complex, involving multiple selection pressures (Perrin and Lehmann 2001; Kokko and Ekman 2002; Matthysen

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2012), many of which can operate in context- or phenotype-dependent ways (Bowler and Benton 2005; Clobert et al. 2009).

The relative contribution of the costs and benefits of dispersal also vary between different systems. For example, the benefits of philopatry are particularly relevant to cooperative breeders, which may gain more in terms of inclusive fitness from becoming helpers-at-the-nest than from becoming opportunistic floaters or establishing a breeding territory in suboptimal habitat (Koenig et al. 1992; Komdeur 1992; Cockburn 2013). However, for noncooperatively breeding species, benefits of philopatry are often restricted to direct benefits associated with family living (see above), which are less likely to outweigh the costs of kin competition (Hamilton and May 1977; Perrin and Lehmann 2001; but see Kokko and Ekman 2002). This lack of indirect fitness benefits means that delayed dispersal can easily yield a net loss to inclusive fitness in noncooperative species (Ronce et al. 1998; Ridley and Sutherland 2002; Gardner et al. 2003). For delayed dispersal to occur under these conditions the costs of dispersal must therefore be heavily compounded by extrinsic factors, suggesting a major role of ecological constraints.

Lizards do not breed cooperatively, but can nevertheless form large complex social groups (Doody et al. 2012; Gardner et al. 2016). For example, species of the Egerniinae (hereafter *Egernia*) represent a continuum of social complexity ranging from solitary to nuclear families to communal family groups, characterized by varying degrees of delayed dispersal (Chapple 2003; Gardner et al. 2016). Targeted experiments within this system offer the opportunity to ask fundamental questions about 1) what drives variation in delayed dispersal and 2) how this may have played a role in the diversification of social systems across the lineage. Here we examined the influence of ecological constraints on offspring dispersal behaviour in a facultatively social lizard, *Liopholis whitii*. *Liopholis whitii* (previously *Egernia whitii*) is a viviparous lizard that forms socially monogamous pair bonds and displays intrafamilial variation in offspring dispersal behavior. Specifically, one or more offspring from a litter can delay dispersal for an extended period of time, residing within the parental home range for up to a year (While et al. 2009a). We used a large-scale captive population experiment to test the influence of habitat saturation on offspring dispersal behavior in *L. whitii* by manipulating the density of conspecifics in available habitat (henceforth habitat saturation). This approach allowed us to directly test the causal relationship between habitat availability and delayed dispersal, providing insight into the factors which may have promoted the initial origins of family living in this taxa.

## MATERIALS AND METHODS

### Study species

*Liopholis whitii* is a medium sized (<100 mm snout–vent length [SVL]) viviparous skink found in dry habitats throughout southeastern Australia. The majority of adults live in small family groups centered on a stable, socially monogamous pair-bond and one or more offspring (Chapple and Keogh 2005; Chapple and Keogh 2006; While et al. 2009a). Mating takes place during the austral spring (September–October) and gestation lasts 3–4 months, with births occurring in the Austral summer (January–February; (While et al. 2007). Offspring within a litter are born over several days (referred to as birthing asynchrony, sensu While et al. 2007).

### Animal capture and husbandry

During November 2014, we captured gravid and nongravid females from a population at Orford on the east coast of Tasmania,

Australia (42°57'S, 147°88'E) using both “mealworm fishing” and noosing techniques and transported them back to university facilities to be housed until birth. In the laboratory we measured individuals for SVL, total length, head length, head width ( $\pm 1$  mm) and mass ( $\pm 1$  mg). Animals were toe-clipped for unique identification.

Adults were housed individually in temperature- and light-controlled rooms, with room lights set to a natural (12:12) day–night cycle. Terraria (30 × 60 × 40 cm) were made from opaque plastic and contained ~5 cm of paper-based cat litter, food, and water dishes, a shelter at one end and a basking rock at the other. Basking lamps were set to come on 1 h after ambient lights came on (simulating sunrise) and turn off 1 h before they went out (sunset). This provided a thermal gradient of 17–40 °C in the terraria, allowing animals attain their preferred body temperature of 34 °C (Bennett and John-Alder 1986). Water was provided *ad libitum* and animals were fed every 2 days on mealworms dusted with mineral supplement and periodically with pureed fruit. Animals were held under these conditions until they gave birth. From January 2015, the terraria of gravid females were checked daily for offspring. Upon discovering offspring, date of birth was recorded and the individual was temporarily separated from its mother to obtain weight ( $\pm 10$  mg), SVL ( $\pm 0.5$  mm), and total length ( $\pm 0.5$  mm). Each offspring was then toe-clipped for unique identification and its birth order in the litter recorded (i.e., 1st born, 2nd born, etc.). Females that gave birth to a single offspring were excluded from the experiment in order to maximize sample size and allow us to investigate the effects of birth order on dispersal behavior. The 30 females used as mothers in the experiment gave birth to a total of 88 offspring. Clutch size ranged from 2 to 4 (average  $2.9 \pm 0.1$ ,  $n_2 = 8$ ,  $n_3 = 16$ , and  $n_4 = 6$ ). Average within-clutch birth spread was  $3.8 \pm 0.3$  days, ranging from 1 to 8 days between females.

### Enclosure Experiments

Following birth, we relocated females and their newly born offspring to large seminatural outdoor enclosures at the Cambridge farm facility and housed them there over a period of 2 months (February–April). Each experimental replicate was comprised of 2 adjacent 8 × 8 m enclosures with identical resources and separated by a partition, creating 6 pairs of one “home” and one “dispersal” enclosure (see Supplementary Figure 1). We installed 3 dispersal gates made of 8-mm mesh in the partition separating each enclosure pair, allowing offspring to move between enclosures within a pair but prohibiting the movement of adults. Each enclosure was provided with identical resources. Five wooden pallets, each covered with ~100 L of burrowing substrate and topped with cement bricks facing each major aspect, were spaced evenly throughout each enclosure, creating 5 high quality crevice sites. This design allowed us to manipulate the degree of habitat saturation in dispersal enclosures by introducing a variable number of adult conspecifics.

We released 5 females and their offspring into each “home” enclosure, giving a total of 30 mothers and 88 offspring included in the experiment. This meant that home enclosures were entirely saturated, with one habitat patch for each female and her offspring. Before release, we attached numbered cloth stickers (Tesa, Germany) to the back of each adult female and a colored bee tag fixed with non-toxic glue (Pender Beekeeping Supplies, Australia) to each offspring for identification. The bee tags were colour coded with 5 different colours corresponding to each of the 5 mothers within a home enclosure. We used the position of a tag along an offspring's back to differentiate which member of a litter it was (i.e., tag fixed to neck = 1st born offspring, middle of the back = 2nd born, pelvis = 3rd born, and base of tail = 4th born) and therefore its unique ID.

We imposed treatments by manipulating the density of adult conspecifics in each “dispersal” enclosure, producing 2 treatments of 3 replicates: 1) a low-saturation treatment where 2 females were released into the “dispersal” enclosures and 2) a high saturation treatment where 4 females were released into the “dispersal” enclosures. Thus, we use the term habitat saturation to refer to population size relative to available resources (sensu Stacey and Ligon 1987), or relative density (e.g., Koenig et al. 1992). All animals allocated to a given enclosure block were released simultaneously. However, enclosure releases themselves were staggered over 3 weeks due to the temporal spread of births between females. As all individuals were recaptured at the same time in April, the duration of the experiment differed between enclosure blocks, ranging from 7 to 10 weeks. Therefore, we alternated releases between treatments to avoid any confounds between treatment and experimental duration. Mothers and their offspring were randomly allocated to treatments before release, resulting in 43 and 45 offspring in the low and high saturation treatments respectively. We did not observe any adult deaths throughout the experiment or find any adult corpses during recapture; however, 3 adults from separate enclosures (all from home enclosures; 2 from low and 1 from high saturation treatment) could not be recovered at the end of the experiment.

### Behavioural observations

We collected positional data and behavioural interactions on all visible individuals twice a day in a morning and afternoon observation session. In each of these sessions we spent 20 min observing each enclosure block, recording which enclosure each individual was in (“home” or “dispersal”) and their physical position within the enclosure. For behavioural observations, we recorded 2 classes of interactions: positive interactions in which individuals were observed basking in physical contact or within a body length of each other with no signs of aggression; and negative interactions in which individuals were observed to chase, bite or wrestle one another (sensu Halliwell et al. *In press*). Afternoon observation sessions commenced at least 4 hours after the completion of morning sessions to reduce spatial autocorrelation. At the end of the experiment we recaptured all mothers and offspring and returned them to the laboratory to measure size, mass and body condition before releasing them back to their initial capture location.

### Estimating home ranges and maternal overlap

During 2 months, we recorded 1365 positional observations. The average number of observations for adults and offspring during our experiment was  $20.6 \pm 1.3$  and  $8.5 \pm 0.9$ , respectively. For adults, we used observational point data to calculate 50% kernel contours via least-squares-cross-validation (LSCV) in the computer program Ranges 9 (Anatrack Ltd, UK). We set a constant LSCV smoothing factor of 0.75 when generating kernels as this was most effective at buffering against over-smoothing and under-smoothing of kernels at the extremes of the sample size range (see Kie 2013). Due to a relatively low number of observations for offspring we were unable to confidently estimate home range kernels, preventing us from assigning delayed dispersal based on mother–offspring kernel overlap. Instead, we used the 50% kernel of each female to identify which crevice site she had utilized as her primary retreat site. After identifying sites occupied by each female, we defined juveniles as overlapping with their mother if 50% or more of their observations were on or within 1 m of that crevice site. This corresponds with the distribution of offspring locations around female crevice

sites in the field (While et al. 2009b; GM While unpublished data). For females with 50% kernels including more than one crevice site, observations of juveniles falling within 1 m of any of these sites were included. Assignment of overlap among those offspring for whom we had enough data to calculate kernel home range (offspring who reached 80% of the home range asymptote; Rose 1982,  $n = 11$ ), was the same whether using the above method or that based on overlap of home range kernels. Offspring assigned as overlapping with their mother based on our point data method had an average of  $79.8 \pm 0.04\%$  of their observations falling within this range, compared to  $12.2 \pm 0.02\%$  for offspring assigned as not overlapping their mother. We excluded offspring with fewer than 3 observations ( $n = 24$ ) from all analyses except those taking “explored” and “survived” as response variables, as the reliability of these responses did not depend on total observation number; a single observation of an individual in the dispersal enclosure is proof of exploration and the recapture of an individual at the end of the experiment is proof of survival. Furthermore, 23 of the 24 offspring excluded from other analyses died early in the experiment, explaining the lack of observations but also providing important data for the survival analysis. Thus, the average number of observations for offspring included in analyses taking “explored” and “survived” as the response was  $8.5 \pm 0.85$ , and for all other analyses was  $11.5 \pm 1.0$ .

### Determining exploration, dispersal, and parent–offspring associations

We defined 2 nonexclusive classes of dispersing individuals, coded as binomial variables, for the purpose of statistical analyses. *Explorers* were offspring who were observed within the dispersal enclosure at least once during the experiment. *Settlers* were offspring observed in the dispersal enclosure in at least 3 sequential observations and never observed back in the home enclosure. Preliminary data analysis showed that 3 sequential observations was sufficient to identify settlers. Specifically, out of 16 individuals who were observed in the dispersal enclosure on 3 sequential occasions, and for whom we have additional observations following this period, only one was observed to return to the home enclosure, representing a 93.5% chance of our criterion correctly identifying a settler.

Delayed dispersal implies a persistent association between parents and offspring within the natal range. Therefore, offspring were only considered to have delayed dispersal if they overlapped their mother’s core home range area (see above). We further reduced this data set to include only offspring who both overlapped and were also observed interacting positively with their mother (number of observed interactions ranged from 1 to 7). These positive associations were easy to identify as offspring were often seen basking directly on top of their mother. Combined, these criteria revealed rates of delayed dispersal comparable to that observed in natural population studies (While et al. 2009a) and experimental contexts (Botterill-James et al. 2016), with 23.9% of offspring (21 offspring from 13 of the 30 clutches) classed as delaying dispersal and 10.2% (9 offspring from 9 of 30 clutches) classed as displaying positive associations. Importantly, although offspring classified as explorers could either go on to settle or delay dispersal, these were not the only possible behavioral responses; offspring could establish a home range within the home enclosure that did not overlap that of their mother, resulting in a negative response for both these categories. Furthermore, settle and delay dispersal were treated as mutually exclusive behaviours; any offspring classified as having settled could not be considered to have also delayed dispersal. This classification

was never contentious, as offspring who settled never had  $\geq 50\%$  of their observations within the maternal home range.

## Statistical analyses

We conducted all statistical analyses in R (Version 3.3.0, 2016), using linear mixed models (LMMs) and generalized linear mixed models (GLMMs) fitted by standard methods in the “lme4” package (Bates et al. 2014). For LMMs, the significance of fixed effects are reported based on  $F$ -tests with degrees of freedom approximated by the Kenward–Rogers method. For GLMMs, the significance of fixed effects are reported based on Wald chi-square tests. To investigate the influence of treatment and phenotypic traits (SVL and release body condition) on offspring dispersal behavior we fit 4 separate binomial GLMMs taking whether or not offspring explored, settled, delayed dispersal and formed positive associations as response variables. We began by including all main effects as well as all pairwise interactions between treatment, SVL, release body condition and birth order as predictor variables. If interaction terms were nonsignificant ( $P > 0.05$ ) they were dropped from the model and results from reduced models are presented. We defined the body condition of each individual from the residuals of a least squares linear regression of body mass on SVL. Body condition values were generated at 2 different time points, once before release into the enclosures and again upon recapture at the end of the experiment.

To examine whether the costs associated with exploration were context-dependent we tested for treatment by exploration interaction effects on growth (i.e., change in SVL) and recapture body condition using Gaussian GLMMs, and survival using a binomial GLMM. For these models we included the pairwise interaction and main effects of treatment and explore as well as the main effect of delayed dispersal as predictors. Release body condition and release SVL were included as covariates were necessary (Table 1 and Supplementary Table 1). We reran all models with positive association instead of delayed dispersal as a predictor to test whether positive interactions with the mother, above and beyond simple home range overlap, were necessary for benefits of philopatry. Due to the low occurrence and survivorship of settlers in the high saturation treatment (see results) we were unable to formally test for treatment by settlement interaction effects on growth, survival, or body condition.

Throughout our analyses we included offspring age and experimental duration (number of days spent in the enclosure) as covariates where relevant to control for the temporal spread of birthing between females and staggered release of animals into enclosures, respectively (See Table 1 and Supplementary Table 1 for full model specifications). We also included enclosure ID as a random factor in all analyses to account for block effects. We checked all data for

violations of model assumptions, including homogeneity of slopes where covariates were used, and all model fits for over-dispersion using a Pearson’s chi-square test. Means and standard errors are reported throughout.

## RESULTS

### Ecological constraints on dispersal behavior

Habitat saturation had no effect on the probability that offspring explored dispersal enclosures (Table 1; Figure 1). However, offspring were less likely to settle in dispersal enclosures in the high compared to the low saturation treatment (Table 1; Figure 1). Offspring that settled in dispersal enclosures were also of smaller body size than those that remained in the home enclosure (Table 1).

Delayed dispersal, whereby offspring established within their mother’s core home range area, occurred at twice the rate in the high (14 offspring) versus low saturation (7 offspring) treatment (Table 1). Delayed dispersal was also positively associated with offspring SVL (Table 1). A significant treatment by body condition interaction indicated that offspring that delayed dispersal in the high saturation treatment were those in poorer body condition at the start of the experiment, whereas this was not the case in the low saturation treatment (Table 1; Figure 2). A similar effect was found for offspring who exhibited positive associations with their mother (Table 1). Birth order had no effect on any aspect of dispersal behaviour (Table 1).

### Costs of dispersal and benefits of philopatry

Out of 88 offspring, 42 survived until the end of the experiment, producing an offspring pre-winter survival rate (48%) comparable to that seen in natural populations (While et al. 2009a) and other captive population experiments (Botterill-James et al. 2016). Exploration was associated with an increase in mortality as well as a loss of body condition among offspring in the high saturation but not the low saturation treatment (treatment:exploration interaction, mortality:  $\chi^2 = 4.67$ ,  $P = 0.03$ ; body condition:  $F_{1, 31.2} = 8.97$ ,  $P < 0.01$ ; Figure 3), indicating elevated costs of exploration at high conspecific density. Habitat saturation also influenced the survival of those individuals that eventually settled dispersal enclosures. Specifically, just one settler survived until the end of the experiment (25% success rate) in the high saturation compared to 8 in the low saturation treatment (73% success rate).

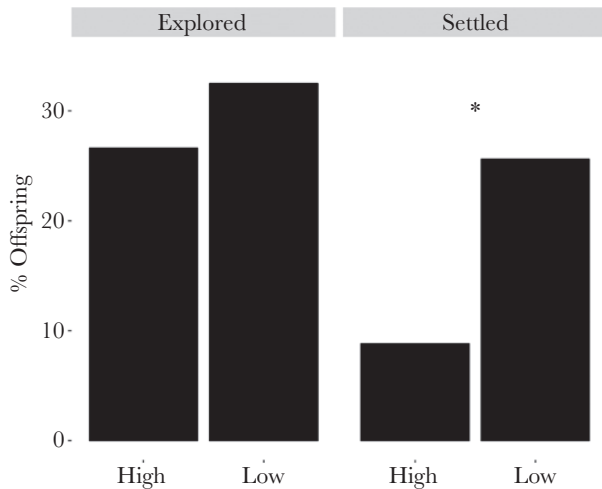
We found no benefits of delayed dispersal itself in terms of offspring growth, body condition or survival (Supplementary Table 2). However, offspring that displayed positive associations with their mother were in better body condition upon recapture ( $F_{1, 32.7} = 5.72$ ,  $P = 0.02$ ). In contrast, positive associations did not

**Table 1**

**The effect of treatment, body size (SVL), and initial body condition on different aspects of offspring dispersal behaviour**

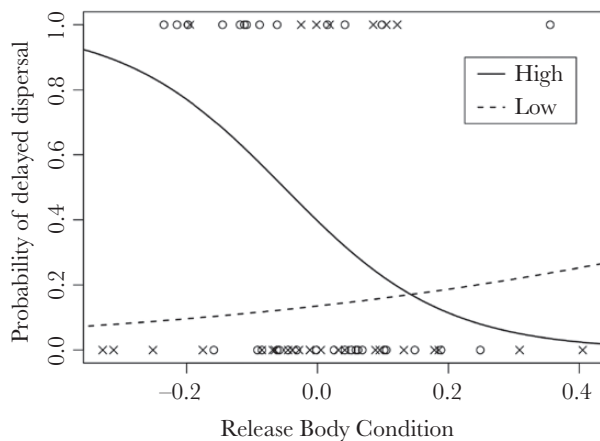
Variable	Explored	Settled	Delayed dispersal	Associated positively
Treatment	$\chi^2 = 0.497$ , $P = 0.481$	<b><math>\chi^2 = 8.304</math>, <math>P = 0.004</math></b>	<b><math>\chi^2 = 4.595</math>, <math>P = 0.032</math></b>	$\chi^2 = 0.240$ , $P = 0.624$
SVL	$\chi^2 = 0.006$ , $P = 0.938$	<b><math>\chi^2 = 4.297</math>, <math>P = 0.038</math></b>	<b><math>\chi^2 = 5.270</math>, <math>P = 0.022</math></b>	$\chi^2 = 0.225$ , $P = 0.635$
Release body Condition	$\chi^2 = 0.279$ , $P = 0.597$	$\chi^2 = 0$ , $P = 1$	<b><math>\chi^2 = 4.479</math>, <math>P = 0.034</math></b>	$\chi^2 = 3.251$ , $P = 0.071$
Birth Order	$\chi^2 = 0.501$ , $P = 0.919$	$\chi^2 = 4.464$ , $P = 0.215$	$\chi^2 = 3.004$ , $P = 0.391$	$\chi^2 = 0.279$ , $P = 0.964$
Treatment * Release body Condition	—	—	<b><math>\chi^2 = 3.871</math>, <math>P = 0.049</math></b>	<b><math>\chi^2 = 4.435</math>, <math>P = 0.035</math></b>
Age (covariate)	<b><math>\chi^2 = 4.721</math>, <math>P = 0.030</math></b>	<b><math>\chi^2 = 4.686</math>, <math>P = 0.030</math></b>	$\chi^2 = 2.541$ , $P = 0.111$	$\chi^2 = 1.323$ , $P = 0.250$

Significant terms are shown in bold. Marginally nonsignificant terms are indicated by a “•” symbol. Dashes indicate interaction terms that were dropped from the model after being found nonsignificant



**Figure 1**

Proportion of total offspring from the high and low saturation treatments that explored and settled in dispersal enclosures. Asterisk indicates a significant difference between treatments in the probability of settlement. See Table 1 for test statistics.



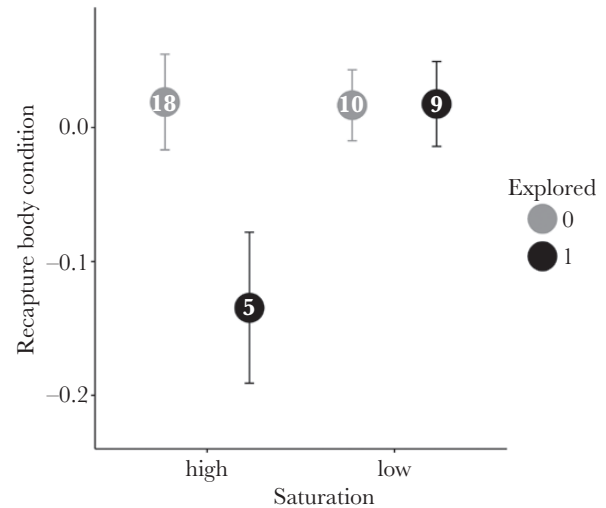
**Figure 2**

Fitted values of the probability of delayed dispersal in relation to release body condition in the high saturation (circles, unbroken line) and low saturation (crosses, broken line) treatments. Probability estimates derived from the binomial GLM described in Table 1. Fitted lines indicate a significant Treatment by release body condition interaction effect in which offspring in the high saturation treatment were more likely to delay dispersal when they had poor body condition upon release. Data restricted to individuals with >3 observations (see methods).

affect the growth ( $\Delta$ SVL;  $F_{1,33.4} = 0.15$ ,  $P = 0.70$ ) or survivorship ( $\chi^2 = 0.39$ ,  $P = 0.53$ ) of offspring.

## DISCUSSION

Our results provide clear experimental evidence that dispersal behaviour and the success of dispersal attempts are directly affected by habitat saturation in a family living lizard. Offspring showed a willingness to disperse when conspecific density was low and habitat vacancies were available, but delayed dispersal when conspecific density was high and when unoccupied habitat was limited. Dispersal movements were also more costly under these conditions, highlighting the role of conspecific aggression in mediating



**Figure 3**

Body condition upon recapture of offspring from the high and low saturation treatments that were and were not observed to explore the dispersal enclosure. Data restricted to individuals that survived until recapture at the end of the experiment. Numbers within points indicate sample size for each group.

offspring dispersal decisions. Taken together these results establish an important link between ecological conditions, delayed dispersal and social organisation.

Habitat saturation did not influence whether or not offspring explored the dispersal enclosures, but it did influence the probability that offspring settled in those enclosures. This suggests a period of cost evaluation during exploration and a willingness to disperse and settle when nearby conditions were favourable. Reductions in relative body condition and an elevated risk of mortality associated with exploration in the high saturation treatment also indicate that the costs of exploring novel habitat increase with increasing conspecific density (e.g., Kingma et al. 2016). These mortality effects are likely be mediated by conspecific infanticide as adult *L. whitii* vigorously defend their territory from conspecifics (Sinn et al. 2008) and actively attack unrelated juveniles (pers obs. G While; B Halliwell), increasing the risks of injury or mortality associated with dispersal movements. Indeed, conspecific aggression is a major cause of offspring mortality in other group living *Egernia* (Lanham and Bull 2000; O'Connor and Shine 2004) and likely contributes to a suite of traits that predispose species of this group to delay dispersal. Costs incurred by intraspecific competition are also often attributable to competition for food or space use. For example, juvenile *Lacerta vivipara* that settle in habitat patches free from conspecifics grow faster and reproduce earlier than those who settle in patches occupied by conspecifics (Le Galliard et al. 2005b; also see Lecomte et al. 1994). Although similar processes are likely to operate in *L. whitii*, we were unable to test for treatment effects on the recapture body condition of settlers due to markedly reduced survival among offspring that settled in high saturation enclosures.

The reduced propensity for offspring to settle in dispersal enclosures in the high saturation treatment corresponded with an increased incidence of delayed dispersal and mother offspring association. This suggests a crucial link between habitat saturation, dispersal costs and delayed dispersal; not only does habitat saturation increase the costs of dispersal, it also increases the incidence of philopatry. Taken together these results provide strong

evidence for a causal link between ecological constraints and social organisation. Lucia and colleagues (2008) demonstrated a similar relationship between conspecific density and delayed dispersal, group formation and group size in prairie voles, *Microtus ochrogaster*, arguing that ecological conditions which influence the social structure of populations may facilitate evolutionary transitions in social complexity. We have previously suggested that these processes could have contributed to divergence in social organisation across the *Egernia* skinks (While et al. 2009b; While et al. 2014). Unfortunately, the short duration of this experiment precludes us from examining long-term consequences of dispersal behaviour on offspring fitness directly. Importantly, however, delayed dispersal may have evolutionary consequences whether or not it presents immediate benefits to offspring; increased association between parents and offspring has the potential to uncover plastic responses in behaviour and allow selection to act on beneficial interactions when they do occur, setting the stage for the emergence of more complex forms of parental behaviour (Uller and Helanterä 2014; While et al. 2014).

What then are the phenotypic predictors of delayed dispersal? Our results indicate that birth order has a negligible effect on offspring dispersal behaviour in this species. This is in line with previous research showing an overall limited effect of birth order on offspring phenotype and survival (While and Wapstra 2008) suggesting that birthing asynchrony may be a mechanism that alters the complete environment within the litter as opposed to the competitive ability of offspring *per se* (While and Wapstra 2008). In contrast, we found body size had a significant effect on offspring dispersal, with small offspring more likely to settle in dispersal enclosures and large offspring more likely to delay dispersal. Furthermore, offspring in poor body condition were more likely to both delay dispersal and display positive associations with their mother, but this effect was only observed in the high saturation treatment. Other studies on lizards have shown that kin competition can promote dispersal of offspring in good body condition, because these individuals are better able to bear the costs of dispersal (Léna et al. 1998; Cote et al. 2007; Cote and Clobert 2010). Therefore, one possible explanation for this treatment by body condition interaction is that the costs of dispersal were so heavily reduced in the low saturation treatment that settlement became a feasible strategy for offspring in poor condition, eroding the relationship between body condition and delayed dispersal observed in the high saturation treatment. Additional data on the phenotypic correlates of dispersal from natural populations of *Liopholis whitii*, as well as other *Egernia* species, will shed further light on this topic.

Benefits of philopatry are well documented among the *Egernia* group. For several species, delaying dispersal to reside within the parental territory provides offspring with protection against conspecific harassment and infanticide (O'Connor and Shine 2004; Sinn et al. 2008; While et al. 2009b), an important source of offspring mortality (Lanham and Bull 2000; O'Connor and Shine 2004). This 'safe haven' effect also allows offspring to utilize key resources within the parental territory that they would otherwise be unable to defend (O'Connor and Shine 2004) and may also have physiological benefits, including redirection of energy from dispersal, vigilance and burrowing behaviors to growth and development (Botterill-James et al. 2016). We found that offspring that delayed dispersal were in better body condition at the end of the experiment than those that did not delay dispersal. However, these benefits were restricted to individuals that also displayed positive social

associations with their mother. This indicates the potential for variable fitness returns between offspring that delay dispersal that depend on the nature of their association with the mother. The mechanisms underpinning the observed differences are currently unknown. One possible explanation is that female *L. whitii* vary the degree of tolerance shown toward different offspring, resulting in differences in the extent to which individual offspring are able to access key resources within the maternal home range. Any benefits of philopatry would then depend on this process.

Offspring dispersal decisions are a product of social context and will be mediated by the resolution of conflict between different agents in the social group. For example, parent-offspring conflict can promote selection for maternal control of offspring dispersal (Starrfelt and Kokko 2010). Female *L. whitii* occasionally chase and even bite their own offspring (pers obs. G While; B Halliwell), suggesting that parental harassment could act as a mechanism to promote offspring dispersal (e.g., Masters and Shine 2003). However, previous captive population studies on *L. whitii* have failed to detect any costs to parents of tolerating offspring within their home range (Botterill-James et al. 2016), calling the motivation for parental harassment into question. Alternatively, competition between siblings over access to the parental home range may underpin dispersal decisions in this system. Our finding that SVL was positively associated with delayed dispersal and negatively associated with settlement suggests an influence of competitive interactions in which larger offspring promote the dispersal of competitively inferior siblings. Finally, offspring may be born with or develop early in life, a behavioural phenotype that promotes or suppresses dispersal behaviour (Cote and Clobert 2007; Vercken et al. 2007; Cote et al. 2010). Importantly, behavioral phenotypes can also be associated with specific morphological adaptations (O'Riain et al. 1996; Sinervo et al. 2006), making it unclear whether differences in the physical characteristics of offspring are a cause or a consequence of dispersal behavior. As our results do not allow us to disentangle the relative contribution of parents, siblings or offspring themselves as mediators of dispersal decisions, this provides an intriguing avenue for future research.

In summary, by manipulating conspecific density this experiment provides empirical evidence for a causal link between habitat saturation and delayed dispersal in a family living lizard. In turn these results support the hypothesis that variation in ecological conditions have been central to the diversification of social organization across the *Egernia* lineage. However, to truly understand the mechanistic drivers of dispersal behavior, we need to integrate knowledge of the costs and benefits of dispersal under different ecological conditions with that of life history traits generating demographic processes conducive to philopatry (Covas and Griesser 2007; Hatchwell 2009). Comparative studies of cooperative breeding birds suggest that long lifespan and high adult survivorship predispose species to delay dispersal by reducing the turnover of reproductive opportunities in the local environment (Arnold and Owens 1998; Arnold and Owens 1999). These life history traits are also characteristic of the *Egernia* (Chapple 2003) and may have facilitated a similar socioecological context conducive to the elaboration of social living. This combination of traits, combined with detailed life history data on a growing number of species, make the *Egernia* group uniquely suitable for comparative studies aiming to connect interspecific variation in social organisation to more general mechanistic drivers of divergence in social systems. Future work testing facultative responses in dispersal behavior to ecological constraints across species that vary in these key

life history traits would be particularly valuable in addressing these aims. Thus, conclusions from this research may apply more broadly, placing feedbacks between life history and ecology at the heart of social evolution in a range of vertebrate groups.

## SUPPLEMENTARY MATERIAL

Supplementary data are available at *Behavioral Ecology* online.

## ETHICS STATEMENT

All work was carried out with approval from the Animal Ethics Committee at the University of Tasmania (Ethics Approval number A14602).

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Data accessibility: Analyses reported in this article can be reproduced using the data provided by Halliwell et al. (2016b).

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