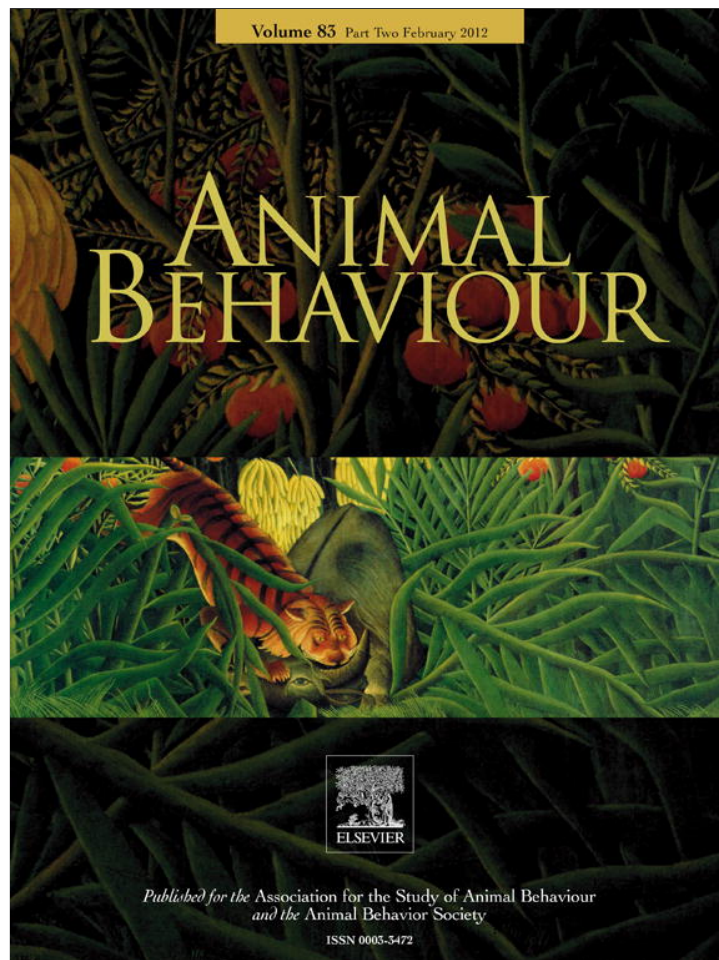


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Natal social environment influences habitat selection later in life

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Habitat selection is an important decision in the life histories of many animals and has implications for many issues in ecology, evolution and conservation biology. Natal experiences may shape adult habitat selection behaviours, but the effects of natal social environment on these decisions are largely unknown. Here we provide an experimental test of the effects of natal social experience on adult habitat selection in the cactus bug, *Chelinidea vittiger* (Hemiptera: Coreidae). We found that females reared in groups were more likely to forage socially as adults than females that were reared alone; however, males consistently avoided joining conspecifics regardless of natal social experience. Our work reveals that cues gathered early in life can have effects that extend across life stages to influence adult habitat selection and social behaviours. Furthermore, the discovery of these patterns in a subsocial invertebrate demonstrates that adult responsiveness to natal social conditions is not restricted to highly social species, and may be common across taxa.

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The influence of early-life events on later adult behaviours has long attracted the interest of biologists, psychologists and the general public (Immelmann 1975; McCord 1979; Hernandez 1986; Aubret & Shine 2008; Blackiston et al. 2008; Janz et al. 2009; Rabin 2009; Sih 2011). In the realm of habitat selection, many adult animals are faced with the challenge of selecting suitable habitat in which to feed and reproduce, and natal experiences may help inform these decisions (Davis & Stamps 2004; Benard & McCauley 2008; Mabry & Stamps 2008; Moreau et al. 2008). These natal experiences may include the use of host plant species, habitat types or substrates (Davis & Stamps 2004). However, the effect of early social experiences on adult habitat selection behaviours is largely unknown. The lack of research on this topic is surprising, because it is well established that early social experiences can affect many other adult behaviours (Nottebohm 1970; Kukuk et al. 1977; Harrison 1980; Hernandez 1986; Champalbert & Lachaud 1990; Irwin & Price 1999; D'Eath 2004; Simpson et al. 2005; Branchi & Alleva 2006; Lihoreau et al. 2009; Sih 2011).

A common social variable in the early life history of many organisms is the size of the family or group in which they are raised. Here, we experimentally tested the influence of this early social variable on the habitat selection decisions of adults. We conducted

this study using the cactus bug, *Chelinidea vittiger aequoris* McAtee (Hemiptera: Coreidae). Both males and females in this species aggregate, yet it is also not uncommon to find solitary individuals (see further details below). Juveniles and adults feed on prickly pear cacti (*Opuntia* spp.), and females use past and current social cues to adjust the number of eggs they lay on cactus spines (Fletcher & Miller 2008). Based on these observations, we hypothesized that these insects adjust their social behaviour based on previous social experiences, and furthermore that these responses can persist across the major life transition from juvenile to adult. We expected social juveniles would be more likely to forage socially as adults, and solitary juveniles would be more likely to forage in solitude. Male and female animals can be affected differently by early-life events, especially for those adult behaviours that directly or indirectly related to sex-specific strategies for reproduction (e.g. Nottebohm 1970). However, here we did not predict sex-specific differences due to early experiences, because both males and females aggregate as adults in the wild (Fletcher et al. 2011).

METHODS

Focal Species

The cactus bug, *Chelinidea vittiger*, is found throughout much of North America where *Opuntia* cacti grow. Females lay eggs end to

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end in neat rows on the underside of cactus spines or other plant material, with observed clutch sizes in our study area ranging from 3 to 10 eggs (R. J. Fletcher, unpublished data). Generations overlap in our study area, such that adults, eggs and juveniles are all present for most of the spring, summer and autumn. *Chelinidea vittiger* nymphs (Fig. 1a) are cryptic and wingless, and rarely move between *Opuntia* patches (Schooley & Wiens 2004). Of 229 patches of cactus observed at the Ordway–Swisher Biological Station (Putnam County, FL, U.S.A.) in the summer of 2011, 88 were found with juveniles. Of these patches, 37 possessed only a single juvenile, while 51 were found with groups ranging between 2 and 13 individuals (mean = 3.9; K. Holmes, unpublished data). Thus, development both in isolation and in groups is common in this species.

Adults may also be found in isolation or in groups. Of 108 cactus patches found with adults in 2011, 91 patches had a single adult, while 17 had between two and four adults (mean = 2.8, K. Holmes, unpublished data). Adult males and adult females aggregate more often than is expected by chance (Morisita index: 4.14 for females, 4.51 for males; $P < 0.001$ for each sex; analyses based on data from Fletcher et al. 2011). Adult cactus bugs fly only rarely, and much dispersal occurs locally via walking (Schooley & Wiens 2004). Adults are cryptic against the sand and leaf-litter under cactus plants, but move up onto cactus pads when feeding. They conveniently leave clear feeding marks that facilitate detecting where individuals have visited and fed (Fig. 1b; Mead & Herring 1974).

Experimental Design

We collected wild cactus bugs (10 males and 40 females) in the summer of 2009 at the Ordway–Swisher Biological Station. In a greenhouse, we paired each male with four females in plastic containers containing potted cacti, and collected the egg clutches

produced. We manipulated clutch size to create two treatments that reflected either natal solitary or social environments: clutches of a single egg or clutches of five eggs. To manipulate clutch size, we obtained clutches of at least five eggs, then removed as many as necessary to create the clutches of a single egg or five eggs. Removal was done by gently dislodging eggs from the plant material to which they had been adhered during oviposition. Resulting clutches were placed into plastic containers (diameter 11.5 cm, height 14.0 cm) each with a single potted cactus pad to allow insects to hatch and develop. We set up rearing containers with cactus and eggs on three occasions: 27 July, 8 August and 24 August 2009.

Between 6 and 8 weeks after hatching, new adults emerged. We isolated new adults from the social treatment within 48 h after their final moult into adulthood. Under natural conditions, cactus bugs commonly remain on their natal host plants for at least 48 h while their new exoskeleton hardens (C. W. Miller, unpublished data). Insects emerging from the solitary treatment were left in isolation within their natal container until habitat selection assays could be performed. We tested adult males and females on a rolling basis in the late autumn of 2009 when they were between 4 and 9 weeks past their final moult. Only one male and one female from each natal container were used for behavioural analyses.

We prepared experimental arenas (Fig. 1c) with l:w:h of 53:38:30 cm with 7.5 cm of topsoil and two size-matched cacti planted, one at each end of the container. Each cactus was made up of two connected cactus pads (i.e. cladodes) with the top pad covered in a mesh bag. A conspecific of the same sex as the focal insect was placed randomly into one of these two bags, and we released the focal insect into the centre of each container on the same day. A mesh and plastic lid was placed over the container, and we returned to count feeding marks as an index of foraging activity after 3 days and after 5 days.

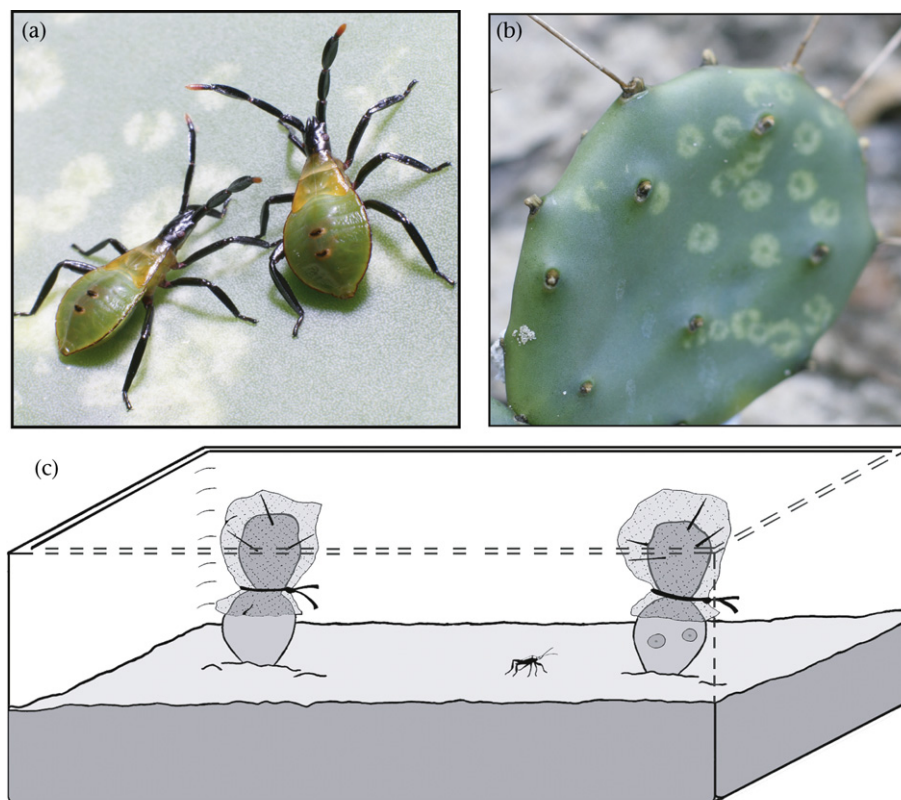


Figure 1. (a) Two cactus bug nymphs on *Opuntia humifusa*, (b) an *O. humifusa* cladode showing typical feeding marks that adults produce and (c) a diagram illustrating containers used to test for the influence of natal social environment on foraging of adult cactus bugs. Photos: C.W. Miller. Illustration: D. Tuss.

Analysis

We used a generalized linear mixed model (GLMM), using a log link function and assuming a Poisson error distribution, to test whether natal environment (reared solitary or socially) influenced foraging patch selection of adults. Because the number of foraging marks is count data, a Poisson distribution was a natural choice for this GLMM; we also considered a negative binomial error distribution, but that model did not converge (Littell et al. 2006). Foraging patch selection was indexed by the number of feeding marks on *Opuntia* with and without a conspecific (patch type, hereafter). Separate analyses were performed on males and females. For each sex, we considered natal environment, patch type and their interactions as fixed effects, and we used Tukey post hoc tests to interpret interactions. Trial (i.e. the individual tested) was included as a random effect to account for repeated measures (foraging marks at days 3 and 5) and the nonindependence of the number of feeding marks on each patch type, thereby focusing on relative differences of individual choices across these days. We did not use binomial proportions (i.e. the proportion of feeding marks on a patch type) because such a model would assume that each feeding mark was an independent observation, which was not the case here. We initially considered egg initiation date and the pairwise interactions of initiation date, natal environment and patch type as covariates to control for seasonal effects. To determine whether these nuisance covariates should be included in the model, we compared models with and without these covariates using Akaike's Information Criterion, adjusted for small sample size (AICc) and provide results from the model with the lowest AICc (Burnham & Anderson 1998; see Appendix, Table A1). To appropriately compare among models, we used Laplace approximation to estimate the marginal likelihood for calculating AICc (Littell et al. 2006). When models had the same AICc score, we selected the simplest model (in terms of the number of parameters in the model). To ensure that biomass differences in cacti were not driving patterns observed in our study, we used a general linear model with the $\ln(\text{mass}_{\text{conspecific}}/\text{mass}_{\text{no conspecific}})$ as the response variable to test for differences in cactus biomass between treatments.

RESULTS

Survivorship was high during this experiment, with 82% of the original group containers producing between three and five adult cactus bugs. We excluded the grouped insects from analyses when group size dropped below three (8%), resulting in 53 individuals (29 males, 24 females) tested in foraging trials.

Overall, we found that natal social environment altered foraging patch decisions of adult females but not those of adult males (Fig. 2). Adult females reared in solitude were more likely to avoid conspecifics than those reared in social environments (natal \times patch type: $F_{1,64} = 9.40$, $P = 0.003$). In contrast, adult males consistently avoided foraging on cactus containing conspecifics (patch type: $F_{1,70} = 17.54$, $P = 0.0001$), regardless of the natal environment in which they were reared (natal \times patch type: $F_{1,70} = 0.27$, $P = 0.608$). For males, the most parsimonious consideration of start date was the inclusion of date (although date \times natal environment also had support; see Appendix, Table A1), where males foraged less as the season progressed (date: $F_{1,70} = 5.86$, $P = 0.018$). For females, the most parsimonious consideration of start date was the inclusion of date and its interaction with natal environment (see Appendix, Table A1), where females were more likely to forage socially later in the year (date \times patch type: $F_{1,70} = 9.40$, $P = 0.0003$). Cactus mass of *Opuntia* containing a conspecific relative to control did not vary

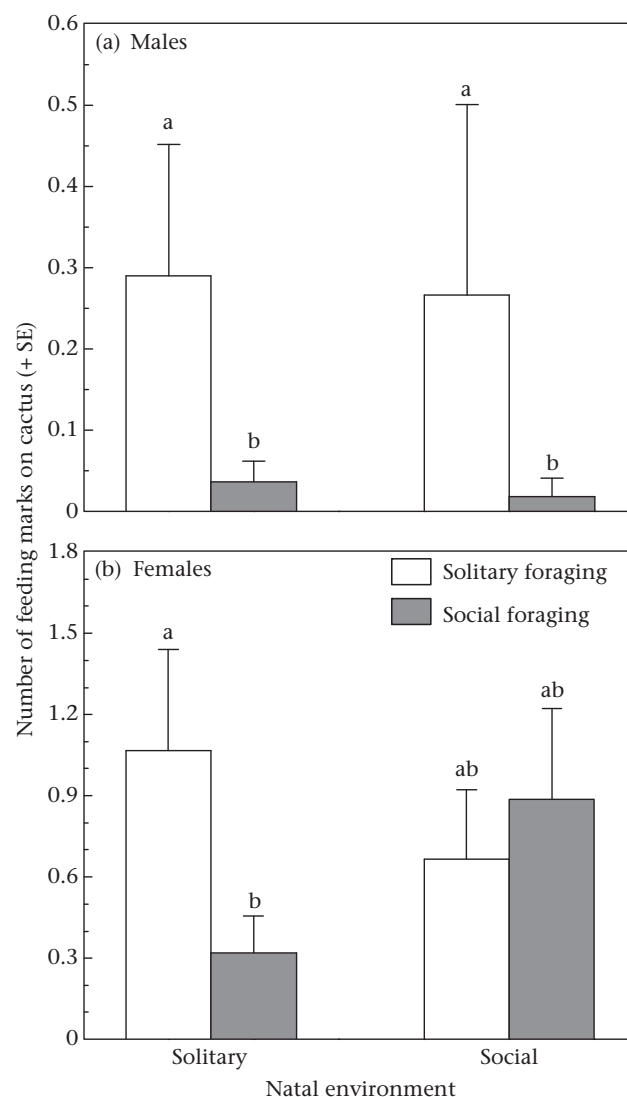


Figure 2. The foraging response, as measured by the number of feeding marks (least squares means \pm SE) of adult (a) male and (b) female cactus bugs to cactus patches containing conspecifics (social foraging) and no conspecifics (solitary foraging), according to the natal environment.

with natal treatment (social group, mean \pm SE: 0.027 ± 0.022 , alone: 0.021 ± 0.028 ; $F_{1,49} = 0.02$, $P = 0.88$).

DISCUSSION

We found that early social experiences affected adult social behaviour in female cactus bugs, but not in males. Adult females reared socially showed no social preference whereas females reared in solitude preferred to forage alone. Previous work has demonstrated that female cactus bugs use social information within a single life stage to guide egg-laying decisions (Fletcher & Miller 2008). Here we found a response that extends across a major life transition and influences adult behaviours many weeks later. Our results suggest complexity and plasticity in the response to early social stimuli, even for species that are not highly social.

Natal family or group size is a simple and common variable in the early life of many animals. Group size can be largely determined by a single female in species where offspring are produced in isolation (e.g. clutch size in noncolonial birds), or by many females when offspring are reared communally (e.g. 'day-care' groups in

giraffe and other ungulates: Estes 1992). In both cases, the natal social environment is influenced by the reproductive behaviours of mothers, and thus the consequences of this environment for offspring phenotypes are partially maternal effects (Moore et al. 1997; Mousseau & Fox 1998). Maternal effects have the potential to persist across generations (Francis et al. 1999; Naguib & Gil 2005). Here, social tendencies may persist if the social rearing environment of females influences (1) clutch size or (2) the production of clutches near existing eggs or juveniles. Because female cactus bugs commonly produce offspring where they forage, the social foraging behaviour witnessed here suggests that such a transgenerational phenomenon may occur.

This study provides one of the first demonstrations that adult habitat selection behaviours can be influenced by the group size in which an animal is reared. Cactus bugs were reared in solitary or social conditions as seen in nature, allowed to moult in their natal environment, isolated, and then tested for social behaviour much later as mature adults, when dispersal is expected. Use of natal cues in making adult decisions may be adaptive for at least two reasons (Davis & Stamps 2004). First, use of natal cues may allow for fast and efficient selection of suitable adult habitat (Stamps & Davis 2006). Here, female cactus bugs reared socially may have associated the presence of conspecifics with suitable habitat, while the cactus bugs reared in solitude did not. Thus, use of social cues may be indicative of the use of natal cues more generally. Second, animals reared in one habitat may simply perform better in similar habitat later in life (Provenza et al. 1998; Akhtar & Isman 2003; Owen-Smith 2003). Foraging patterns, vigilance for predators, bacterial symbionts and up-regulation of enzymes needed for solitary or social feeding may be established early in life, and re-establishing the social environment may lead to better performance (Stamps & Davis 2006).

Regardless of the evolutionary causes of this phenomenon, its presence may have both ecological and evolutionary consequences. Early social conditions (or lack thereof) may modify movement and habitat selection, and thereby metapopulation dynamics, local adaptation and sympatric speciation (Davis & Stamps 2004; Benard & McCauley 2008; Stamps et al. 2009). Thus, like natal habitat, early isolation may have consequences for many current problems in both basic and applied research.

Females responded to early social experiences, so why did males consistently avoid one another? One possibility is male territoriality. Males in this family of insects (Coreidae) often form aggregations at larger spatial scales, yet compete for small territories within the aggregations (Mitchell 1980; Eberhard 1998; Miyatake 2002), reminiscent of a hidden-lek mating system (Wagner 1998; Fletcher & Miller 2006). While male–male competitions have not been witnessed in this particular species, individual male cactus bugs may achieve fitness benefits by spreading out within larger aggregations, regardless of early life experiences.

The effect of natal social experiences on later adult behaviours is a special case of social information use. Prior research has demonstrated that social information, information extracted from interactions with, or observations of, other organisms (Wagner & Danchin 2009), can have powerful effects within a single life stage, modifying decisions ranging from foraging to reproductive allocation (Kendal et al. 2004; Dall et al. 2005; Nocera et al. 2006; Seppänen et al. 2007; Danchin et al. 2008; Fletcher & Miller 2008). Fewer studies, in contrast, have examined the influence of social information across life stages, especially for species that are not highly social (but see McFarlan 1966; Harrison 1980; Simpson et al. 2005; Lihoreau et al. 2009). Here, we found effects of early social information that not only carried across life stages, but that also persisted for several weeks past the point of isolation. In fact, the amount of time spent in isolation as an adult was

approximately equal to the amount of time spent in the natal treatments, yet the effect of natal environment persisted. These patterns indicate that individuals may somewhat 'imprint' on their natal social experience.

In summary, this study demonstrates that early social experiences can affect adult habitat selection decisions. These findings, from a subsocial invertebrate, suggests that social responsiveness may occur in a wide range of species, not just those that are highly social. Furthermore, these effects may persist late into life and even shape behaviours of future generations.

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Appendix

Table A1

Model selection including start date as a covariate when testing the effect of natal environment on foraging by adult *C. vittiger*

Model	Females			Males		
	–2LL	AICc	ΔAICc	–2LL	AICc	ΔAICc
No date covariate	317.08	327.78	12.91	163.19	173.82	4.34
Date	317.03	330.02	15.15	156.6	169.48	0.00
Date*patch type	299.53	314.87	0.00	156.54	171.73	2.25
Date*natal	316.76	332.10	17.23	154.29	169.48	0.00

–2LL: deviance ($-2 \times \log$ likelihood); AICc: Akaike's Information Criterion, adjusted for small sample size; ΔAICc: AICc for model *i* minus the minimum AICc in the candidate models shown here.