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The type and timing of social information alters offspring production

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The acquisition and use of information are essential for decision-making in an uncertain world. The use of social information, or information from the behaviour of others, may be a common and efficient mechanism to improve estimates of resource quality by animals. According to theory, social information cues with higher information content should have a greater influence on decision-making, and current information should be weighed more than prior information. However, experimental tests of these hypotheses remain scarce. We exposed female cactus bugs (*Chelinidea vittiger*) to different types of social information (the presence of conspecific eggs or nymphs) presented at different times (current or prior to egg laying) to determine the influence of social information on offspring production. We found that social information substantially altered the number of eggs produced. The presence of conspecific eggs, regardless of timing, consistently increased egg production, whereas nymphs only increased egg production when present during egg laying. We conclude that the type and timing of social information may have an important, yet unappreciated, influence on reproductive allocation.

1. INTRODUCTION

Animals live in an uncertain world. To reduce uncertainty, animals use various types of information in decision-making, including both personal (i.e. direct interactions with the environment) and social (i.e. the behaviour of others; Dall *et al*. 2005). Public information, or information from the performance of others (Danchin *et al*. 2004), is one form of social information used to improve the estimates of resource quality, which has been documented in a wide range of taxa (e.g. Valone & Templeton 2002). Public information is thought to be particularly useful because it integrates numerous factors regarding resource quality. Such information can guide many behaviours, including foraging, habitat selection and mate choice, and can have profound effects on the ecology and evolution of organisms (Danchin *et al*. 2004). Other social information, such as the presence of conspecifics ('location

cues' of Danchin *et al*. 2004), can also provide useful information that may be more frequently available than public information (Nocera *et al*. 2006).

Conceptual frameworks and theoretical models for information use draw heavily from the idea that animals integrate both prior and current information to guide decisions (e.g. Dall *et al*. 2005; Fletcher 2006). Presumably, current information should be weighed more than prior information because information reliability degrades over time (van Bergen *et al*. 2004; Seppänen *et al*. 2007). Models also predict that social cues with more information content should be used more than cues with less information content (Doligez *et al*. 2003; Koops 2004). Unfortunately, few experiments have isolated how animals process and use different types of social information (Bonnie & Earley 2007; but see Doligez *et al*. 2002; Fletcher 2007).

Here, we examined whether individuals use different types of social information, available at different times, to guide offspring production in the cactus bug (*Chelinidea vittiger aequoris* McAtee), a hemipteran that feeds, breeds and aggregates on prickly pear cactus (*Opuntia* spp.; Mead & Herring 1974). We assumed that the presence of eggs and juveniles would provide social information to female cactus bugs (*Chelinidea vittiger*) regarding resource quality, based on their aggregative behaviours and a previous experiment suggesting increases in egg production in the presence of nymphs (C. W. Miller 2007, unpublished data). We predicted that the information with high content regarding quality (the presence of juveniles) would be used as a stronger positive stimulus than the information with lower content (the presence of eggs). The presence of juveniles should provide higher information content than eggs by demonstrating that offspring have hatched and survived on the resource (public information), whereas eggs only provide information that other female(s) selected the resource for oviposition (location cues). We also predicted that current information should be used as a stronger stimulus than prior information, which was tested by providing social information cues either before or during mating and reproduction.

2. MATERIAL AND METHODS

(a) Focal species

Chelinidea vittiger aequoris McAtee is found throughout most of the United States and Mexico where *Opuntia* occurs. In the study area, females generally begin producing and depositing eggs on cactus spines (figure 1) in early March and continue egg laying through September, with two or more generations produced per year (Mead & Herring 1974). Importantly, generations overlap (Mead & Herring 1974), such that females may encounter eggs and nymphs, acting as potential information cues, while laying their own eggs. Nymphs are wingless and rarely move between *Opuntia* patches (Schooley & Wiens 2004).

(b) Experimental design

Juveniles and gravid females were captured in north central Florida (29.4° N, 82.0° W) during the autumn of 2007, and kept in laboratory colonies with ample *Opuntia humifusa* cactus available. Upon reaching the final nymphal instar, first and second generation laboratory animals were isolated with a single *Opuntia* cladode (i.e. a cactus pad) to complete development, reach sexual maturity and remain unmated until the start of our experiment.

We used a randomized block design to assess the influence of the type and timing of social information on egg production. Conspecific eggs were used as location cues and nymphs were used as public information cues. For the timing of social information,
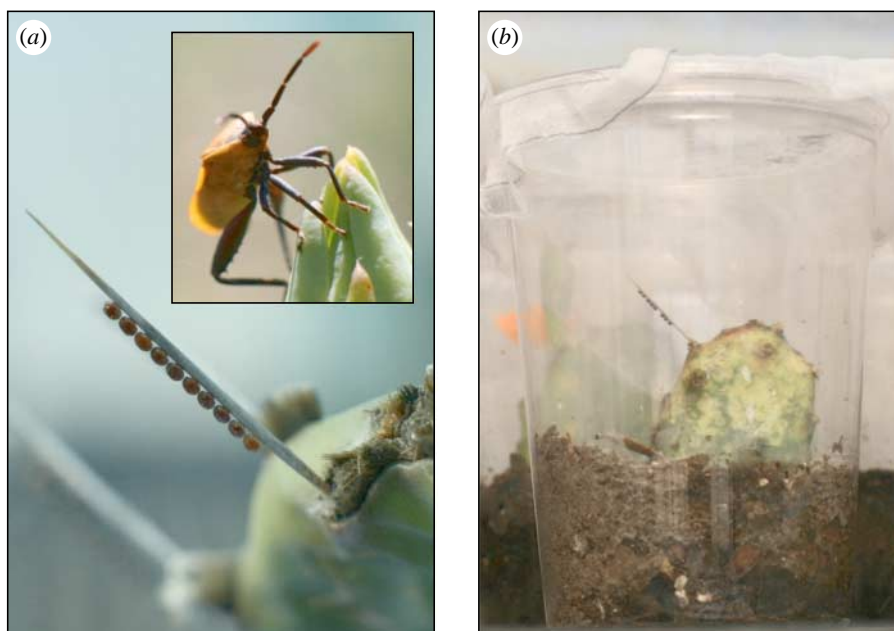
Figure 1. (*a*) An adult *Chelinidea vittiger aequoris* McAtee on *Opuntia* and a cactus spine with social information cues from the presence of conspecific eggs. (*b*) An example container used to test for the influence of social information on offspring production by *C. vittiger aequoris* McAtee. Photo credit: C. W. Miller.

cues were presented before mating and reproduction (prior information) or during mating and reproduction (current information). Overall, we considered four treatment combinations—eggs prior, eggs current, nymphs prior and nymphs current—and one control (no information cues presented).

In March 2008, we manipulated information cues in individual plastic containers (10×15 cm) fitted with mesh screen in the lid (figure 1*b*). We used two greenhouses with two blocks/greenhouse (temperature range: 4–40°C). Each treatment included 17 replicates (four to five replicates per block). In each container, we placed 5 cm of top soil and planted one cladode. We removed all spines from the cladodes except for one, standardized at a 45° angle near the top of the cactus (figure 1*b*). We next assigned each container to an experimental treatment. For the egg prior treatment, we added a mature, egg-producing female to each container to lay a clutch. We then removed the females after one week and standardized clutch sizes to five eggs. For the nymph prior treatment, we added five third-instar nymphs. The control and current information treatments were unmanipulated at this stage.

Next, we randomly placed a virgin female in each container for one week. We subsequently removed social information cues from the prior treatments and added social information cues to the current treatments. To add egg cues to the current treatments, we cut spines off of all cacti and randomly shuffled the spines to new containers (including controls). The spines with eggs from the egg prior treatment were randomly moved to the egg current treatment. Nymphs from prior treatments were removed from the containers (some had moulted) and new third-stage nymphs were used for the current nymph treatment. We then added a male to each container to allow mating opportunities.

After a 2-day mating period, we monitored egg production daily over a 5-day period (total mating/egg production period of one week). Following this time, males, females and information cues were removed from the containers. After three additional weeks, we counted hatched eggs to estimate the number of eggs fertilized. *Chelinidea vittiger* eggs normally hatch within 9–12 days (Mann 1969).

(c) *Analysis*
Prior to analyses, we removed experimental units where the cactus ($n=5$) or the female ($n=4$) suffered mortality before the termination of the experiment ($n=78$ for analyses). We used generalized linear mixed models to test for effects of the type of information (egg, nymph or no information), the timing of information (prior, current or no information) and their interaction on three response measures: (i) the probability of producing eggs over the 7-day period, (ii) the number of eggs produced, and (iii) the proportion of eggs that hatched. In each analysis, we treated greenhouse and block (greenhouse) as random effects. For probability responses, we used a logit link function and assumed binomial

errors; for the number of eggs produced, we used a log link function and assumed Poisson errors.

3. RESULTS
Overall, 41 out of the 78 females produced eggs during the experiment ($n=431$ eggs produced, 78.6% hatched). Neither the type nor the timing of social information substantially influenced the probability of females laying eggs ($F_{1,73} < 0.42$, $p > 0.51$; figure 2*a*). The total number of eggs produced, however, was substantially influenced by the type of social information available (figure 2*b*; $F_{1,73} = 9.34$, $p = 0.003$), depending on the timing of social information availability (type × timing: $F_{1,73} = 6.91$, $p = 0.011$). Pairwise contrasts, controlling for among-block variation, decompose this interaction: the presence of nymphs as prior information was not different from controls ($F_{1,73} = 0.14$, $p = 0.71$), but all other treatments caused 42–74 per cent more offspring production relative to controls ($F_{1,73} > 5.04$, $p < 0.03$). Finally, the proportion of eggs hatched did not vary with either the type or the timing of social information ($F_{1,36} < 2.32$, $p > 0.13$; figure 2*c*).

4. DISCUSSION
We found that both the type and the timing of social information influenced the quantity of offspring produced by *C. vittiger aequoris* McAtee. From these results and other recent research (e.g. van Bergen *et al.* 2004; Fletcher 2007), it is becoming increasingly clear that social information use can be complex and dynamic, with numerous consequences for individuals, populations and communities (Giraldeau *et al.* 2002; Danchin *et al.* 2004; Fletcher 2006; Seppänen *et al.* 2007).

We predicted that the presence of nymphs would provide richer information than that of eggs, and that *C. vittiger aequoris* McAtee should respond more
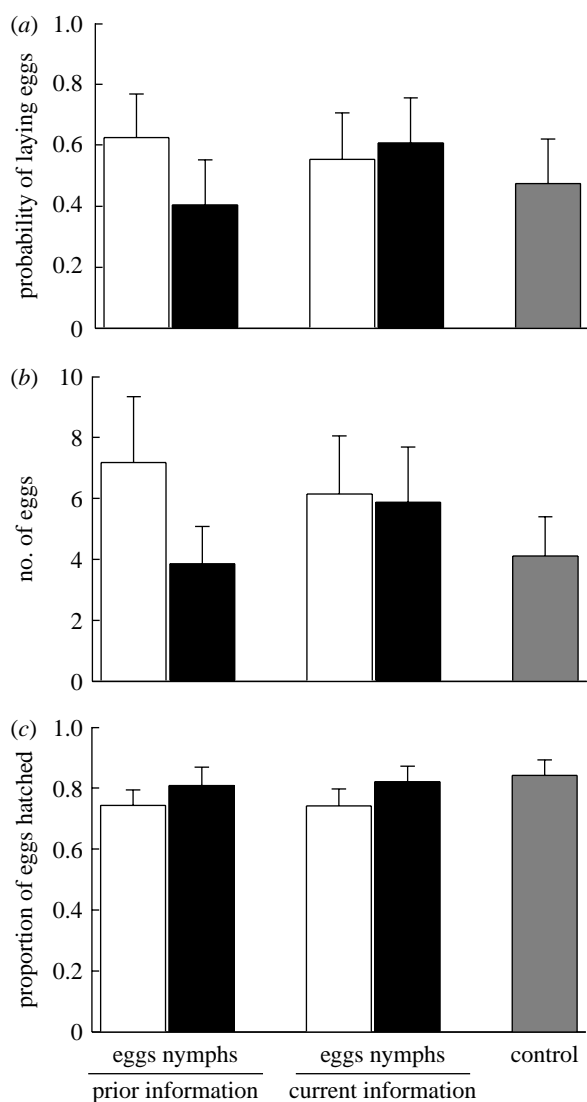
Figure 2. The response of *Chelinidea vittiger* to the type and timing of social information. (*a*) The probability of egg laying ($\pm$s.e.), (*b*) the total number of eggs produced and (*c*) the proportion of eggs hatched across treatments and controls.

strongly to social information that is currently available during mating and egg production than to information provided prior to these events. Nymph cues were used when available currently but were not used when available prior to mating, supporting our timing prediction. However, conspecific eggs were used consistently regardless of timing. Why would eggs and nymphs be used differently, depending on timing? Although nymphs in the prior treatment could provide information on resource quality, their subsequent removal may have been a cue of predation risk, effectively cancelling out any information regarding resource quality. Eggs, by contrast, are smaller and more cryptic to predators, thus egg removal may provide a weaker cue to adult insects. Alternatively, *C. vittiger aequoris* McAtee could have primarily been using only 'location' information provided by eggs and nymphs; nymph prior information had the oldest information regarding oviposition location choices among treatments. Finally, nymphs from the prior treatment may have produced

mixed public and personal information cues. These nymphs had more time to feed on the cactus, possibly degrading its quality via competition (as described in some other insects; e.g. Schoonhoven 1990), whereas nymphs in the current treatment were only beginning to feed as females produced eggs; thus, the resource may have been perceived as higher quality. These explanations suggest that either social information content varies over time or that animals integrate personal and social information differentially depending on the timing of information.

These results are, to our knowledge, the first to examine the use of public information in reproductive allocation. Yet, recent experiments have highlighted that other forms of information can influence other investment decisions, such as sex ratio allocation (e.g. Forsman *et al.* 2008). As the field of information ecology continues to develop, we should look more broadly at the dynamic use of information on a wide range of decisions and the consequences for individuals, populations and communities.

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