The Science of Nature (2023) 110:20
https://doi.org/10.1007/s00114-023-01847-8

ORIGINAL ARTICLE

Wild social behavior differs following experimental loss of vision in social hermit crabs

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Received: 26 August 2022 / Revised: 20 February 2023 / Accepted: 2 May 2023 / Published online: 18 May 2023

Abstract

Even for animals with multiple senses at their disposal, there may be a strong reliance on a single sense, like vision, for social behavior. Experimentally blocking or eliminating vision offers a powerful means of testing impacts on social behavior, though few studies have followed experimentally blinded individuals in the wild to test potential changes in social behavior in natural settings. Here we conducted experiments with social hermit crabs (*Coenobita compressus*), applying opaque material overtop their eyes to temporarily blind individuals. We then released these experimentally blinded individuals and non-blinded control individuals into the wild as well as into captive social settings. Compared to control individuals, experimentally blinded individuals initiated significantly fewer social contacts with conspecifics in the wild. These experimentally blinded individuals were not, however, differentially targeted by conspecifics. Interestingly, unlike the wild experiments, the captive experiments showed no differences in social behavior between experimentally blinded and non-blinded control individuals, suggesting that experiments in natural settings in the wild may be essential to fully unraveling impacts of blindness on social behavior. Broadly, for social animals that are highly reliant on the visual modality, social behavior may change dramatically if they lose their vision.

Keywords Vision · Sensory loss · Social behavior · Wild and captive experiments

Introduction

Social groups would be unable to form if individuals were incapable of detecting one another (Ward & Webster 2016). Hence, there is a fundamental causal link between the ability to detect conspecifics and sociality. A wide range of different sensory modalities exist to detect conspecifics (Stevens 2013). Yet even with multiple senses at their disposal (Rebora et al. 2018; Ward & Mehner 2010), some animals may be highly reliant on a single sense, becoming disproportionately invested in this one specific modality (Herbert-Read et al. 2010; Laughlin et al. 1998). For example, for animals heavily invested in vision, they may be skilled at visually detecting conspecifics (Dollion et al. 2022), but may show more limited capabilities with other sensory modalities (Cronin et al. 2014). Hence, one potential consequence for social animals that are highly reliant on the visual modality is that social behavior may change dramatically if they lose part or all of their vision.

Organisms can naturally lose their vision either through physical damage to their eyes (Poscai et al. 2017) or when environmental sources of light become limited (Valdes & Laidre 2018). Physical damage to one or multiple eyes can occur due to fights (Clutton-Brock et al. 1979), predation events (Grisley et al. 1996), old age (Cepurna et al. 2005; Land & Nilsson 2012), or diseases and parasites (Ruehle & Poulin 2019). Partial or total loss of vision can also be the result of an organism entering an environment devoid of light (Johnsen 2012) or a setting in which opaque objects act as visual obstructions (Steele & Laidre 2019). Upon losing vision, a visually oriented organism may have difficulty successfully locating and acquiring information from nearby conspecifics (Callaghan et al. 2012). In addition to such

Communicated by: Matthias Waltert

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difficulties, other conspecifics could perceive the blinded individual as weaker, and thereby alter how they interact with that individual (Bacqué-Cazenave et al. 2017; Kaplan et al. 1993). Thus, the reduction or loss of vision could have complex impacts on social behaviors, potentially leading to either a reduced ability to initiate social contact, to altered social treatment by fellow conspecifics, or both.

Experimentally blocking or eliminating vision provides a powerful means of testing what, if any, changes in social behavior result. Yet rather than permanently damaging eyes, there exist less invasive and more nuanced ways of temporarily knocking out an individual's vision by experimentally "blinding" it (e.g., using a blindfold: Anderson et al. 1996). Studies deploying experimental "blinding" techniques have been conducted both in the wild and in captivity, with many of the wild studies focusing on migratory behavior (e.g., Botton & Loveland 1987; Streng & Wallraff 1992) and usually only the captive studies focusing on detailed social behavior (e.g., Pellis 1996). For example, in captive studies on both crayfish and lobsters, experimentally "blinded" individuals significantly decreased how often they initiated social interactions when placed in an arena with another conspecific (Bruce et al. 2018; Callaghan et al. 2012; Kaplan et al. 1993). Such experiments reveal that vision loss can impact social behavior, but their focus on captive dyadic interactions does not enable exploration of the full ramifications of vision loss in more complex social settings found in the wild. Conducting experiments in the wild can provide deeper insights into how and why vision loss may impact an individual's social behavior as well as how other conspecifics interact with that individual.

Highly social terrestrial hermit crabs (*Coenobita compressus*) offer a promising system to test how experimental loss of vision may impact social behavior in the wild. These social hermit crabs (Laidre 2012a, b, 2013a; Krieger et al. 2020) roam a flat beach environment in search of ephemeral social groupings of conspecifics. Free-wandering individuals continually move between groups (Laidre 2014), which dissolve and recombine in a fission–fusion arrangement (Couzin & Laidre 2009). Prior experiments in the wild have simulated a wide variety of visual social cues, revealing that social hermit crabs are highly reliant on vision (Laidre 2010, 2013a, 2018a, b; Bates & Laidre 2018; Steele and Laidre 2019; Doherty and Laidre 2020, 2022; Steele and Laidre 2023). For example, when environmental debris in the form of fallen leaves accumulates along the beach, it can constrain individuals' ability to locate social groups (Steele & Laidre 2019). Yet, to date, no experiments have been conducted on temporarily blinded individuals to examine potential changes in social behavior, both by the blinded individuals themselves and by conspecifics toward those that are blinded. Notably, because social hermit crabs exist in an extremely competitive "housing market" of architecturally remodeled shells (Laidre 2011; Laidre & Vermeij 2012; Laidre et al. 2012, 2018b, 2019a, b), individuals are constantly assessing and probing conspecifics to find weaker individuals they may be able to evict, thereby allowing them to "move up" in the housing market (Laidre 2021a, b, c). In theory, temporarily blinded individuals might not only be more limited in their ability to initiate social interactions with others, but might also be perceived as weaker or disadvantaged, potentially facing increased social harassment from conspecifics.

Here we conducted experiments on social hermit crabs, using experimentally blinded focal individuals to test the hypothesis that vision loss would impact social behavior. Specifically, we hypothesized that vision loss would change how focal individuals interact with others as well as how others interact with such focal individuals. This "vision loss" hypothesis makes two key predictions: (i) Experimentally blinded focal individuals, due to their impaired sensory abilities, will be less adept at initiating contact with conspecifics and locating social groups. (ii) If other conspecifics detect that an experimentally blinded focal individual has lost its vision and is therefore weaker or disadvantaged, such focal individuals will become targets of increased social harassment and testing by conspecifics. These predictions were experimentally tested in the wild and in captivity.

Methods

Study site and system

We conducted experiments in Osa Peninsula, Costa Rica, on Piro beach (8°23′33.1″N 83°19′50.3″W), where the highly social terrestrial hermit crabs (*Coenobita compressus*) have been under long-term study (Laidre 2010, 2019a). Our experiments were carried out along the beach-forest interface during February and March 2018. All our experiments (both in the wild and in captivity) were conducted by ES during morning hours (0500–1000), a time of peak social activity in which free-wandering individuals are activity roaming the beach, visually searching for conspecifics. We randomly selected individuals between 10 and 16 mm shell diameter that were wandering the beach and then randomly allocated them between three different conditions. Final sample selections were thus made in an unbiased manner.

Three conditions

To test the impact of vision loss on social behavior, we conducted a series of experiments with three different conditions (two control conditions and one experimental condition; Fig. 1). Each condition involved placing material, which varied between either transparent or opaque, overtop the eyes, then testing individuals within minutes after this

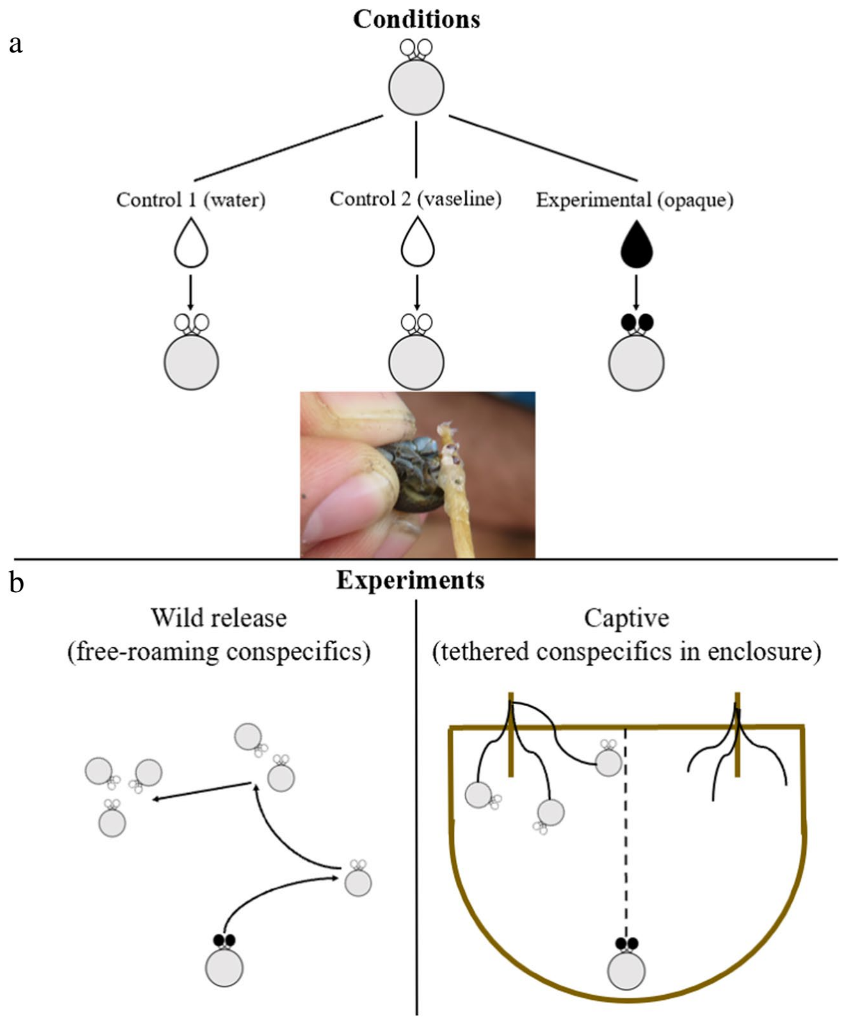

Fig. 1 Design for testing the impact on social behavior of experimental loss of vision in highly social terrestrial hermit crabs (*Coenobita compressus*). **a** Schematic of the three conditions: control 1 (water), control 2 (Vaseline), and experimental (opaque) were applied to cover both eyes of focal individuals ($n=20$ per condition). Only the experimental condition temporarily "blinded" focal individuals (see Table 1). Below is a picture of control 2 being applied to the eyes of a hermit crab. **b** Experiments were then conducted both in the wild and in captivity. In wild experiments, focal individuals were released onto the beach, where they could interact with other free-roaming conspecifics, as indicated by the solid lines. In captive experiments, focal individuals were placed into an enclosure (divided equally into halves by the dotted line), where one side (randomized) had a simulated social group of three tethered conspecifics and the other side had the same materials but no social group

application. Across conditions, we applied the materials in the same manner, holding the focal individual slightly out of its shell, and using a toothpick to place a small dab of the material overtop both eyes (Fig. 1a). For the two control conditions, we used freshwater (control 1) and Vaseline (Vaseline® Intensive Care™ Petroleum Jelly; control 2). Neither of these controls blocked vision, but it is possible that the Vaseline control had some refractive impact on light and could therefore potentially reduce spatial acuity in individuals. For the experimental condition, we used an opaque charcoal face mask (Shills©; experimental), which had the same viscosity as Vaseline but which, because it was opaque, experimentally blinded the individual. Previous experiments that placed substances more volatile than charcoal onto the carapace of hermit crabs observed no adverse impact to visually guided behaviors (Laidre 2010). Additionally, previous observations of hermit crabs dusted by charcoal from a nearby fire showed no difference in ability to navigate their environment. Therefore, the opaque charcoal face mask should not impact chemically guided behaviors and only affect visual capabilities when completely covering the eyes. Individuals attempted to clean both the Vaseline and opaque charcoal face mask off their eyes but were incapable in the timeframe of the experiments. Lastly, due to the structure of the crustacean compound eye being a hardened mineralized cuticle, both the Vaseline and opaque charcoal face mask did not act as an irritant when placed on the surface of the eye (Alagboso et al. 2014; Greco et al. 2013; Peisker and Gorb 2010). Confirmatory tests (see below) substantiated that the three conditions influence individuals' vision as intended.

Confirmatory tests with visual scares

To confirm whether the experimental condition did indeed blind individuals, and whether the control conditions left individuals' vision intact, we used visual motion stimuli to provoke an innate and consistent defensive shell-retraction response, which we refer to as visual scare experiments. These experiments tested whether individuals responded to standardized scare stimuli by ducking into their shells: if they respond, it confirms their vision is intact; whereas if they do not respond, it confirms they are temporarily blinded. Our visual scare experiments involved both overhead and horizontal tests. For the overhead test, each individual was placed in an opaque cup (approximately 3 cm diameter) and then after the individual emerged from its shell, the experimenter moved one hand overtop the opening of the cup. For the horizontal test, each individual was placed on the ground and then after the individual emerged from its shell, the experimenter moved a large shell (a 24.5 mm *Nerita scabricosta* shell attached to a dowel) directly toward the individual in its frontal view. Across all three conditions (control 1, control 2, and experimental), we tested $n = 20$ individuals per condition using these scare stimuli (for a total of $n = 60$ total individuals). Each individual was tested in three separate trials using the overhead scare, as well as in three separate trials using the horizontal scare. Only if an individual failed to respond across all three trials did we deem it "blinded." The results (see Table 1) confirmed that the two control conditions left individuals' vision intact, while the experimental condition "blinded" 18 out of 20 individuals.

Experiments on vision and social behavior

To test whether vision loss impacts social behavior, we tested a total of $n = 120$ individuals ($n = 60$ in wild experiments and $n = 60$ in captive experiments). For both wild and captive experiments (Fig. 1b), individuals were randomly allocated across the three conditions (control 1, control 2, and experimental), with $n = 20$ individuals tested per condition. After having been treated, individuals were then tested in randomized order across conditions. At the end of each experiment, we collected the focal individual, confirmed that the condition was still present on the eyes, and then completely removed all materials from the individual's eyes with freshwater. Individuals that had already been tested were stored together in a large tub for the entire duration of all trials and were provided with both food and freshwater. After all the experiments were completed, the hermit crabs were released back to where they were collected from in the wild. There were no discernible differences between individuals from different conditions, since by this point all material had been removed from their eyes and all individuals behaved similarly.

Table 1 Percentage of individuals in each different condition that responded to two different visual scare stimuli ($n = 20$ per condition)

Condition	Overhead scare	Horizontal scare
Control 1 (water)	100%	100%
Control 2 (vaseline)	100%	100%
Experimental (opaque)	0%	10%

Wild experiments

To test the impact of vision loss on social behavior in the wild, we released focal individuals onto the beach at randomized locations, allowing them to freely interact with other conspecifics in the wild. Upon placing a single focal individual onto the ground, the experimenter then moved to the forest and observed the focal individual from a distance with binoculars. Once the focal individual first emerged from its shell and began moving, the trial started. Each trial then lasted 5 min, during which the experimenter quantified each of the following social interactions (see Doherty and Laidre 2020, 2022): "approach" (i.e., the focal individual and a conspecific came within one shell length of one another); "contact" (i.e., the focal individual and a conspecific made physical contact); and "piggyback" (i.e., the focal individual or a conspecific climbed on top of the other's shell). Approaches could not be distinguished based on who initiated the approach, since the paths of the focal individual and other conspecifics often intersected without any clear initiator. However, contacts could be distinguished based on whether they were initiated by the focal individual, by another conspecific, or by both simultaneously. Likewise, piggybacks could be distinguished based on whether they were initiated by the focal individual or by another conspecific. The total number of each different social behavior was recorded across the entire trial, then divided by the observation time to calculate a rate. During the wild experiments, not all focal individuals could be tracked for the full 5 min (Table S1), since occasionally individuals would evade the observer's line of sight by retreating under fallen foliage (e.g., leaves: Steele and Laidre 2019). However, across conditions, there was no significant difference in the amount of time individuals were tracked (Kruskal–Wallis test: $H_2 = 2.88$, $p = 0.24$; Fig. S1).

Captive experiments

To test the impact of vision loss on social behavior in captivity, we placed focal individuals into an enclosure with a simulated social group. The enclosure, which was placed directly on the beach, was constructed from bendable plywood and consisted of an arena (933 cm^2 area) shaped into a half ellipse (Fig. 1b), with natural beach sand on the ground. Above the ground, a string was positioned along the center of the arena (10 cm from the ground), dividing it visually into two separate sides, which were monitored by the experimenter. For each trial, a simulated social group of three live, tethered conspecifics (see Laidre 2010; Steele and Laidre 2019 for methods) was randomly placed on one of the two sides of the arena. The other side of the arena had the same materials (dowel and fishing line), but no conspecifics.

A single focal individual was then placed in the arena within a small (approximately 3 cm diameter) clear container. This container was positioned at the far end of the arena, away from the simulated social group, and along the line that divided the arena into two sides. Once the container was lifted, the trial started. Each trial then lasted 5 min, during which the experimenter quantified each of the following behaviors by the focal individual: (a) which side of the arena the focal individual first moved toward (group side or not); (b) time to approach the group (i.e., how long, up to the maximum cutoff time of 5 min, till the focal individual came within a shell length of a conspecific); (c) total time on group side (i.e., how long the focal individual spent on the side of the arena with the group); and (d) number of contacts with the group (i.e., how many instances of physical contact occurred between the focal individual and its conspecifics). All focal individuals could be tracked for the full 5-min trial in these captive experiments.

Statistical analyses

If vision loss does impact social behavior, then social behavior should differ across the three conditions. In particular, the experimental condition (in which focal individuals are experimentally blinded) should differ from one or both of the control conditions (in which focal individuals have intact vision). To test our predictions (see "Introduction"), we therefore compared the experimental condition with each of two control conditions separately. Since data from both wild and captive experiments were not normal and could not be transformed, we used non-parametric tests (Wilcoxon tests) to compare the experimental condition with each of the control conditions. In addition, for the captive experiments, we used Pearson's chi-square test to compare what side of the arena focal individuals first moved to and whether or not they approached the simulated social group. All statistical analyses were performed in JMP® Pro 15.2.1 (SAS Institute, Cary, NC, USA), with the overall alpha level controlled at 0.05 and with the Bonferroni method used when undertaking multiple tests.

Results

Wild experiments

For wild experiments, social behavior differed significantly between the experimental and the control conditions (Table 2). Compared to the controls, the experimental condition showed significantly fewer focal-initiated contacts and piggybacks (Wilcoxon test of focal-initiated contacts for experimental v. control 1: $Z=4.44$, $p<0.0001$; experimental v. control 2: $Z=3.31$, $p<0.0009$; Fig. 2b; focal-initiated piggybacks for experimental v. control 1: $Z=3.78$, $p<0.0002$; Fig. 2c). Notably, "blinded" focal individuals did not initiate a single contact or piggyback. Furthermore, contacts initiated simultaneously by both parties were either significantly reduced (Wilcoxon test of experimental v. control 1: $Z=4.08$, $p<0.0001$; Fig. 2b) or were at least marginally lower (Wilcoxon test of experimental v. control 2: $Z=2.55$, $p=0.01$, non-significant after a Bonferroni correction). Interestingly, there was a marginal trend of increased contacts and piggybacks initiated by other conspecifics toward the focal individual (Wilcoxon test of other-initiated contact for experimental v. control 1: $Z=2.26$, $p=0.02$; Fig. 2b; other-initiated piggybacks for experimental v. control 1: $Z=2.12$, $p=0.03$; Fig. 2c; though both tests were non-significant after a Bonferroni correction). Overall, therefore, the wild experiments showed that vision loss significantly reduced focal-initiated social behavior, though had, at best, only a limited impact on the social behavior focal individuals received from conspecifics.

Captive experiments

For captive experiments, there was no difference in social behavior between the experimental and control conditions (Table 3). In particular, there was no difference in what side individuals first moved toward (Pearson's chi-square test: $\chi^2=1.74$, df $=2$, $p=0.42$; Fig. 3a) or in the total time individuals spent on the side with the simulated social group (Fig. 3c). Compared to the controls, experimentally blinded

Table 2 Social behaviors during wild experiments. Some social behaviors (e.g., contacts) could be initiated by focal individuals, by other conspecifics, or by both simultaneously. Wilcoxon tests comparing between conditions ($n=20$ per condition). *NS* = non-significant after a Bonferroni correction

Comparison	No. of approaches (per min)	No. of contacts (per min)			No. of piggybacks (per min)	
		Focal	Other	Both	Focal	Other
Experimental v. control 1	$Z=1.17$, $p=0.24$	$Z=4.44$, $p<0.0001$	$Z=2.26$, $p=0.02$ (NS)	$Z=4.08$, $p<0.0001$	$Z=3.78$, $p<0.0002$	$Z=2.12$, $p=0.03$ (NS)
Experimental v. control 2	$Z=0.71$, $p=0.48$	$Z=3.31$, $p<0.0009$	$Z=0.35$, $p=0.72$	$Z=2.55$, $p=0.01$ (NS)	$Z=0.00$, $p=1.00$	$Z=0.84$, $p=0.40$

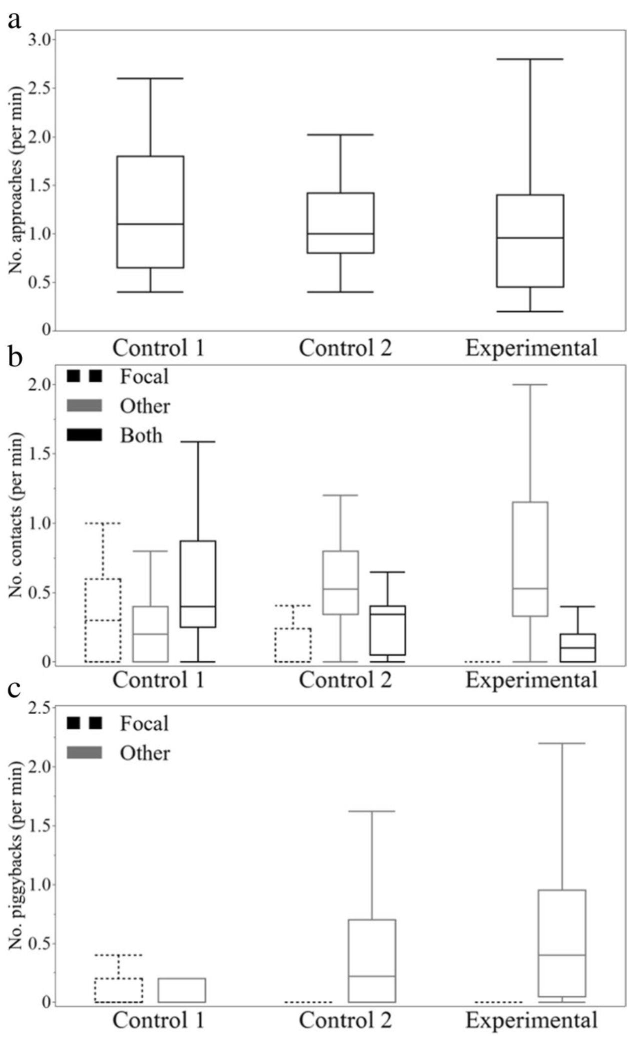

Fig. 2 Social behaviors during wild experiments. Across the three conditions: **a** number of approaches (per min) between focal individuals and other conspecifics. **b** Number of contacts (per min) initiated by focal individuals, by other conspecifics, or by both simultaneously. **c** Number of piggybacks (per min) initiated by focal individuals or by other conspecifics. Box plots display the following: interquartile range (box), median (horizontal line within box), and 1.5*IQR (whiskers). $n = 20$ individuals tested in each of the three conditions. See Table 2 for statistical comparisons between conditions

individuals took a longer time to approach the social group and made fewer contacts with the social group (Wilcoxon test of time to approach group for experimental v. control 2: $Z = 2.00$, $p = 0.05$; Fig. 3b; number of contacts with group: experimental v. control 2: $Z = 2.01$, $p = 0.04$; Fig. 3d; though both tests were non-significant after a Bonferroni correction). Across conditions, there was no difference in whether individuals approached or never approached the social group (Pearson's chi-square test: $\chi^2 = 2.85$, df $= 2$, $p = 0.24$). Indeed, the majority of individuals did not approach the social group (Table 4). Interestingly, across all conditions, individuals spent approximately half the available time on either side of the enclosure (Fig. 3c). Overall, therefore, the captive experiments, in contrast to the wild experiments, showed no detectable difference in social behavior.

Discussion

Previous experimental studies manipulating animals' vision have focused on captive dyadic encounters (e.g., Bruce et al. 2018; Callaghan et al. 2012; Kaplan et al. 1993), rather than on wild polyadic encounters, which implicate greater social complexity (Ward & Webster 2016). Here we used social hermit crabs as a system to experimentally "blind" focal individuals and then test the impact on social behavior, both in wild and captive settings. We examined how focal individuals interacted with conspecifics as well as how conspecifics interacted with focal individuals. Interestingly, wild and captive experiments produced disparate results: in captivity, "blinded" individuals exhibited no difference in social behavior, whereas in the wild, "blinded" individuals showed a significant difference in social behavior. In particular, "blinded" individuals in the wild reduced how often they initiated contact with conspecifics, though there was no difference in the number of contacts they received from conspecifics. Overall, temporary vision loss can thus impact social behavior, with experiments in both the wild and captivity being crucial to resolving these impacts.

Captive experiments can be useful because they allow for the precise control of many external variables and also provide an easier way to observe focal individuals (Hollén & Manser 2007; Männiste et al. 2013). However, there are possible artifacts associated with captivity (Griffith et al. 2017), which may change animals' behavior for reasons other than the primary focus of the experiments. Consequently, studies in captivity may sometimes be limited in what conclusions they can draw about key changes in social behavior (Boal & Gonzalez 1998). In our study, even though social hermit crabs were directly collected from the wild and also tested within a semi-natural enclosure, which

Table 3 Social behaviors during captive experiments. Wilcoxon tests comparing between conditions ($n = 20$ per condition). *NS* = non-significant after a Bonferroni correction

Comparison	Time to approach group (min)	Total time on group side (min)	No. of contacts with group
Experimental v. control 1	$Z = 1.15$, $p = 0.25$	$Z = 0.54$, $p = 0.59$	$Z = 1.43$, $p = 0.15$
Experimental v. control 2	$Z = 2.00$, $p = 0.05$ (NS)	$Z = 0.09$, $p = 0.92$	$Z = 2.01$, $p = 0.04$ (NS)

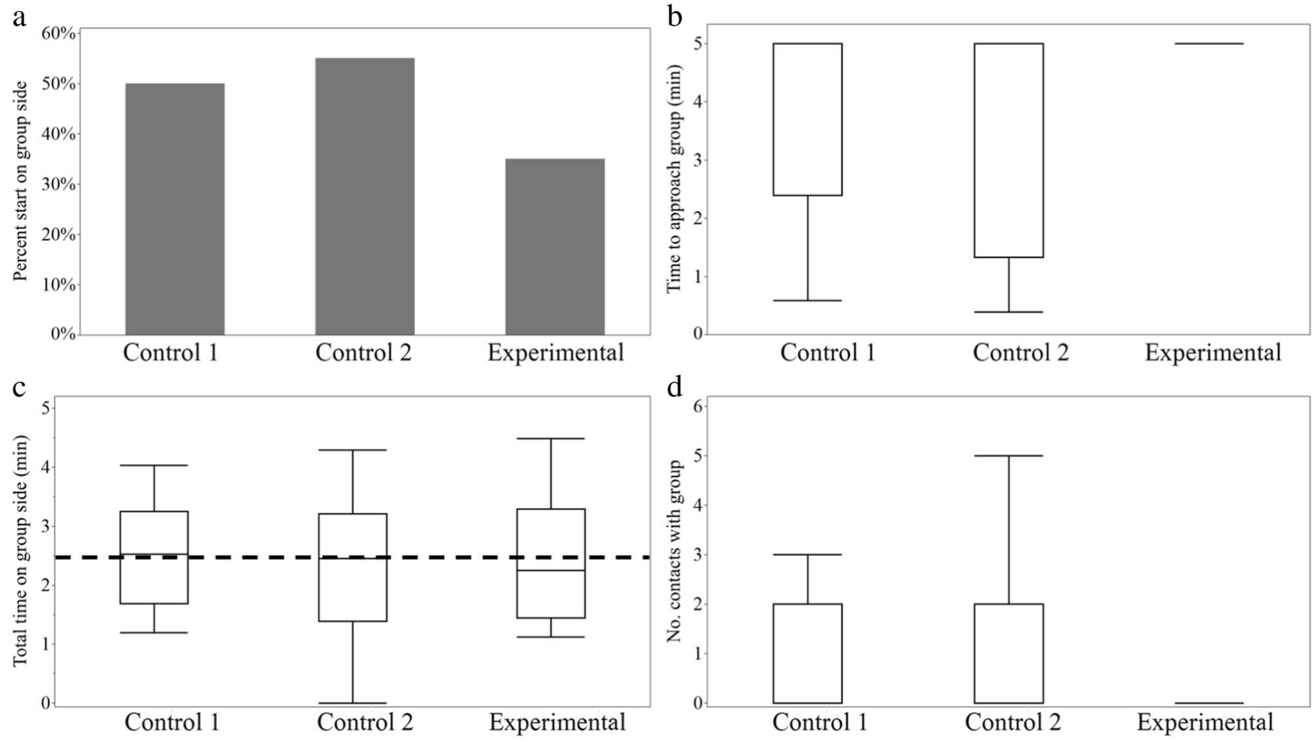

Fig. 3 Social behaviors during captive experiments. Across the three conditions, social behavior by focal individuals toward the simulated social group: **a** percentage of focal individuals that moved first toward the side with the group. **b** Time (in min) to approach the group. **c** Total time (in min) spent on the side with the group (dotted line indicates half the total trial time). **d** Number of contacts with the group. Box plots display the following: interquartile range (box), median (horizontal line within box), and 1.5*IQR (whiskers). $n = 20$ individuals tested in each of the three conditions. See Table 3 for statistical comparisons between conditions

had natural beach sand as its substrate, the "blinded" and "non-blinded" individuals displayed no difference in their social behavior. Specifically, few of the focal individuals in captivity even approached the simulated social group, despite this very same stimulus being highly attractive to individuals in the wild (see Laidre 2010; Steele and Laidre 2019). Moreover, across all conditions in captivity, focal individuals spent approximately half of the trial time on each side of the enclosure, thus showing no preference between sides. Interestingly, many of the focal individuals in captivity were observed simply circling the enclosure, in an apparent attempt to get out. One plausible explanation, therefore, for the lack of interest in interacting with the simulated social group could be that handling (Doherty & Laidre 2022) and then confining specimens in captivity changes their motivation to attempting to escape their enclosure (see Krieger et al. 2020). This apparent change in motivation highlights the importance of conducting *both* wild and captive experiments, since the weakness of either one can be complemented by the strengths of the other, allowing the two to mutually inform one another.

Table 4 No. of individuals that never approached the simulated social group during captive experiments ($n = 20$ per condition)

Condition	Never approached social group
Control 1	13
Control 2	11
Experimental	16

While losing a sensory modality may be detrimental, some organisms are capable of coping with the loss by utilizing another modality (Herbert-Read et al. 2010; Rebora et al. 2018; Starnberger et al. 2018). Yet, not all organisms use such "backup" modalities (Cely Ortiz and Tibbetts 2021; Stevens 2013). One reason may be that, even if other modalities exist as potential "backups," they can sometimes be insufficient, especially over certain distances. For example, our results suggest that social hermit crabs, upon losing their vision, have difficulty initiating contact with conspecifics, which may be because their other modalities (like olfaction, e.g., Valdes and Laidre 2019) function best over longer distances and are less effective at shorter distances, which necessitate vision. Animals may also become reliant on single modalities if, over evolutionary time, one modality has proven highly robust, with low chances of it ever being completely lost (Cronin et al. 2014; Laughlin et al. 1998). For example, with respect to vision, many organisms can protect their eyes (Cronin 1986; Poscai et al. 2017), have a backup eye if one is lost (Land & Nilsson 2012; Menda et al.

2014), regrow an eye that is damaged or completely removed (Egger et al. 2007; Ventura et al. 2019), or clean natural materials off their eyes if they ever become covered (Honegger et al. 1979). Once organisms become so specialized upon a singular modality, then if it is ever compromised, they may be unable to use an alternative modality and may have difficulty performing essential tasks (Holland et al. 2005; Stevens 2013). Future comparative work should contrast different species to determine what key environmental variables are linked to a greater reliance on single versus multiple modalities, especially the extent to which individuals can cope when one or more of these modalities are experimentally lost.

The difference we found in social behavior between "blinded" and "non-blinded" individuals could have been exacerbated by the short trial times within our experiments. For example, complete vision loss might have been shocking initially, causing "blinded" individuals to focus their attention during the 5-min trials on removing the opaque material from their eyes and simply cease locomotion or exploration. However, our wild trials only began after focal individuals emerged from their shells and began moving; and while the exact displacement of individuals was not quantified, "blinded" individuals never remained stationary, but rather continued to wander around their environments with the opaque material still on their eyes. Nevertheless, it remains possible that individuals may need more time to cope with an initial shock of complete vision loss. Perhaps given enough time, individuals that have lost all visual capabilities might find other ways to resume social interactions with conspecifics, including using other sensory modalities, regardless of whether or not they represent imperfect "backups." Social hermit crabs have an excellent sense of smell on land (Krieger et al. 2021) and use these acute chemosensory abilities to detect recently deceased conspecifics (Valdes & Laidre 2019). However, it is unclear if olfaction could ever represent a viable alternative modality for locating and contacting live conspecifics, particularly at close range. Further work should test if, over longer time periods, "blinded" individuals remain limited in their ability to initiate social contact or can instead find another means of coping with complete vison loss.

Notably, there was no strong indication that "blinded" individuals became social targets for others or experienced increased levels of harassment by conspecifics. Nevertheless, it remains possible that wild conspecifics might eventually assess that "blinded" individuals are weaker over longer periods. Critically, tracking individuals in the wild for periods longer than the current experiment is challenging due to a matrix of leaves and other materials under which individuals can disappear from view (Steele and Laidre 2019). However, if "blinded" individuals could be tracked over hours or days, they might have difficulty finding food (Laidre 2013b) or navigating their physical environment (Doherty and Laidre 2022), which could translate to additional weakening on top of their blindness. If they lacked any coping mechanisms, then "blinded" individuals might eventually be surrounded by coalitions that could evict them from their shells (Laidre 2021c). Such a fate would be hard to avoid if blinded individuals could not even see others coming for them and thus could not avoid negative forms of social interaction. Ultimately, the extent to which an individual can cope with vision loss (Cronin et al. 2014) may feedback to the level of harassment it receives from conspecifics (Ward & Webster 2016), especially over extended periods. Broadly, future work should explore the importance of vision loss for social behavior over longer durations, especially in the wild, and consider interactions and their outcomes from both the perspective of the blind and from their seeing conspecifics.

Conclusions

Previous work has tested the consequences of vision loss on social behavior in captive settings; yet, few studies have examined the impact of vision loss in both more complex wild and captive settings. Here we studied social hermit crabs, *Coenobita compressus*, which rely on vision to locate ephemeral social groupings. By experimentally blocking vision and releasing blinded and nonblinded individuals in both wild and captive settings, we show that individuals that lose visual capabilities initiate significantly fewer social contacts in the wild, but exhibit no difference in social behavior in the captive setting. Therefore, animals may experience important changes in social behavior if vision is lost, and conducting both wild and captive experiments may be crucial when testing behaviors such as sociality.

Acknowledgements We thank all members of the Laidre lab, including Clare Doherty, Jakob Krieger, and Leah Valdes, as well as Osa Conservation staff for assistance in the field. All experiments were approved by the Costa Rican Ministerio de Ambiente y Energía (MINAE).

Author contribution ML conceived the idea for the study and designed the experiments; ES carried out the experiments and collected all the data; both authors jointly analyzed the data and wrote the manuscript.

Funding This work was supported by an EEES/GAANN fellowship to ES and Dartmouth College startup funds to ML.

Data availability All data are provided in the Electronic Supplementary Material.

Declarations

Ethics approval This research was conducted in compliance with international, national, and/or institutional guidelines for the care and study of invertebrates.

Conflict of interest The authors declare no competing interests.

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