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Individual Recognition in the Olive Nerite Snail *Neritina reclivata* (Neritopsina: Neritidae) as Determined by Clustering Behavior

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ABSTRACT

We tested the ability of the olive nerite snail (*Neritina reclivata*) to discriminate between familiar and unfamiliar individuals by observing the individual with which they formed clusters with. Our control group consisted of 15 snails that were housed together in the same tank throughout the experiment. We used the control group to observe the clustering behavior of the snails without exposing them to unfamiliar conspecifics or unfamiliar territories. The control group set the benchmark for our expectations of clustering among other individuals. For the experimental group, we placed five familiarized snails of the same color into a tank with 10 unfamiliar snails of a different color. Five out of seven clusters (on average) during a given phase had excessive amounts of minority colored snails. This indicates that, when placed in a new territory with novel individuals, snails tend to form clusters with familiar individuals and thus provides the first evidence of individual recognition in *N. reclivata*. This work presents new insight into the ecology of *N. reclivata*, with special emphasis on intraspecific interactions.

INTRODUCTION

Individual recognition is the ability of an organism to recognize a familiar individual (whether related or not) using cues learned through prior association with that individual; the individual can then be identified as a competitor, neighbor, mate, offspring, or sibling (Gherardi et al., 2010). Individual recognition can be adaptive in relation to parental care, schooling behavior, aggressive behaviors (including cannibalism), nepotism, and mate choice (Schausberger, 2007) as well as predator avoidance and communal breeding behaviors (Carreno et al., 1996). Kin recognition is the biased treatment of conspecific individuals based on genetic relatedness (Schausberger, 2007). Kin recognition is adaptive in avoiding inbreeding, reducing aggression between relatives, raising young, and securing resources. Individual recognition and kin recognition may overlap in the mechanisms used to identify them, which include prior association (or familiarity) and phenotype matching (Schausberger, 2007). Phenotype matching occurs when an individual learns something about its own phenotype based on odor, vision, etc. and compares it to others to determine whether they are related or unrelated (van der Jeugd et al., 2002).

Kin recognition occurs in many invertebrate species, but individual recognition is less extensively researched. Gherardi and Tiedemann (2004) demonstrated binary individual recognition in the hermit crab *Pagurus longicarpus* by demonstrating that they could categorize individuals into two subgroups. Additionally, big-clawed snapping shrimp (*Alpheus heterochelis*) are capable of discriminating between former mates and unfamiliar conspecifics (Ward et al., 2004). Although many animals exhibit kin or individual recognition, few studies have examined these abilities in snails.

Many animals, social or nonsocial, have been observed forming aggregates. Clustering behaviors decrease vulnerability to dehydration and predation, which increases mate availability (Prokopy and Roitberg, 2001). Stimuli known to evoke grouping among cockroaches include light, temperature, and relative humidity (Prokopy and Roitberg, 2001). Male cockroach nymphs exhibit significantly faster development when grouped with conspecific males than when alone (Holbrook and Schal, 1998). Clustered males have a higher probability of encountering females compared to isolated males, and this is particularly prevalent when the overall population density is low (Prokopy and Roitberg, 2001).

The olive nerite snail, *Neritina reclivata*, is irregularly distributed along coastal regions in the Gulf of Mexico and Caribbean Sea (Lehman and Hamilton, 1981). Detailed information about snail dispersal is limited (Zealand and Jeffries, 2009), but snail movement and clustering can be determined by tidal rhythms (Moulton, 1962). Three species of *Nerita* (*N. polita*, *N. japonina*, *N. taxis*) form clusters, and trail following has been demonstrated in many intertidal mollusks (Focardi et al., 1985). Dispersal ability depends on landscape structure which can create movement barriers and/or corridors. Landscape composition also influences the rate of movement between populations, and snails have relatively low rates of movement (Wilmer et al., 2008). For example, only 28 of 1130 spring snails were identified as immigrants from one connected spring to another (Wilmer et al., 2008). Therefore, it is not likely that there is selection pressure for individual recognition based on dispersal rate. However, it could be advantageous for snails to recognize familiar individuals to decrease inbreeding.

Our study addresses individual recognition in *N. reclivata* snails by examining clustering behavior. The purpose of our study is to determine whether *N. reclivata* can recognize familiar individuals and form clusters based on these identifications. We tested whether snails could discriminate between familiar and unfamiliar individuals by observing whether snails formed clusters with familiar (previously associated) individuals as opposed to clustering with unfamiliar snails.

METHODS

We conducted our research at Millikin University in Decatur, IL in 2011. We obtained *N. reclivata* from the Carolina Biological Supply Company. We maintained snails in de-chlorinated water and fed them fish food *Ad libitum* once per week. After two weeks of acclimation, we randomly as-

signed each snail into one of three groups designated Batch 1, Batch 2, or control. Each snail was marked on its shell with non-toxic purple, orange, or green paint as follows. Batch 1 consisted of three aquaria (19.05 cm L x 11.43 cm W x 13.97 cm H) - one designated purple, one orange, and one green - with 15 snails each. Batch 2 was an exact replica of Batch 1: it contained three tanks, designated purple, orange and green, with 15 snails in each tank labeled as described above. The seventh tank was the control tank, which contained 15 snails labeled 1-15 in purple.

We tested the experimental groups in seven different phases (Table 1). The experiment began with phase 1 (referred to as the home phase). The first time we performed the home phase, 15 snails of the same color were given 48 hours in their original tank (tank of their designated color) to familiarize themselves with like-colored individuals. In every other phase, we moved 5 individuals from their original tank and introduced them to a new tank of 10 snails for 48 hours. Each phase involved the movement of 5 individual snails from their original tank to an unfamiliar tank. When initially placed in a novel tank, we positioned individuals in the same corner of the tank but not close enough together to be considered a cluster. After we moved the first 5 individuals to a new tank for 48 hours, we repeated the home phase, and returned snails to their original tank for 24 hours. After 24 hours back in their original tank, we moved those same 5 individuals to a second unfamiliar tank for 48 hours. For example, in phase 2, purple individuals 1-5 were moved to the green tank for 48 hours, then returned back to the purple tank for 24 hours, then moved to the orange tank for 48 hours (Table 1). Every three hours for the duration of the research, we observed and recorded the interactions and clusters formed between snails. Each phase lasted 48 hours, with the exception of the home phase. We repeated the home phase at the completion of every phase to allow the snails to re-acclimate. The snails in the control group remained in the same tank for the duration of the experiment.

During each observation period, we photographed and drew all individuals in each tank to document snail positions. For ease of recording, we divided each tank into seven regions. For statistical purposes, we defined a cluster as two or more snails in a group and set our significance level at $P < 0.025$. We adopt $P < 0.025$ instead of 0.05 because we reused majority snails in some trials (see Materials and Methods). To overestimate the impact of this reuse, we applied the simplest and most conservative adjustment to account for multiple comparisons – the Bonferroni correction (Dunn, 1961). In this case, we apply a Bonferroni correction of 2, leading to the more restrictive significance criterion of $P < 0.05/2$.

Table 1. Experimental phases 1-7 with *Neritina reclivata* individuals that were transferred listed as 1-5, 6-10, 11-15. Each phase lasted 48 hours, with phase 1 (home phase) being repeated for 24 hours between each phase.

Phase 1 (**home phase**)	Purple (**1-15**)	Green (**1-15**)	Orange (**1-15**)
Phase 2	1-5 **purple** moved to **green tank**	1-5 **green** moved to **orange tank**	1-5 **orange** moved to **purple tank**
Phase 3	1-5 **purple** moved to **orange tank**	1-5 **green** moved to **purple tank**	1-5 **orange** moved to **green tank**
Phase 4	6-10 **purple** moved to **green tank**	6-10 **green** moved to **orange tank**	6-10 **orange** moved to **purple tank**
Phase 5	6-10 **purple** moved to **orange tank**	6-10 **green** moved to **purple tank**	6-10 **orange** moved to **green tank**
Phase 6	11-15 **purple** moved to **green tank**	11-15 **green** moved to **orange tank**	11-15 **orange** moved to **purple tank**
Phase 7	1-15 **purple** moved to **orange tank**	11-15 **green** moved to **purple tank**	11-15 **orange** moved to **green tank**

Table 2. Batch 1 experimental Phases 2-7 where orange snails (*Neritina reclivata*) accounted for 1/3 of the population. Columns 3 and 6 show the number of instances in which statistically significant clusters formed, and the total number of snails of colors 1 and 2 that were part of each cluster group in the following format: number of significant clusters (number of majority color: number of minority color). The *P*-values in Columns 4 and 7 indicate the likelihood of these results happening by chance.

Phase	**Color 1** (10 individuals)	**Color 1 excess**	***P*-value 1**	**Color 2** (5 individuals)	**Color 2 excess**	***P*-value 2**
2	Purple	1 (16:0)	$1.52*10^{-3}$	Orange 1-5	4 (3:0), (2:0), (2:2), (2:2)	$3.61*10^{-4}$
3	Green	3 (17:2), (36:9), (6:0)	$3.49*10^{-5}$	Orange 1-5	1 (11:0)	$5.60*10^{-6}$
4	Purple	1 (4:0)	0.20	Orange 6-10	1 (9:0)	$5.08*10^{-5}$
5	Green	2 (59:2), (6:0)	$7.28*10^{-10}$	Orange 6-10	3 (10:4), (2:0), (2:1)	$8.27*10^{-5}$
6	Purple	2 (25:0), (8:0)	$1.55*10^{-6}$	Orange 11-15	3 (19:0), (2:0), (5:5)	$1.31*10^{-11}$
7	Green	2 (6:0), (2:0)	0.04	Orange 11-15	1 (19:0)	$8.6*10^{-10}$

RESULTS

We used the control group as a reference point to determine the standard clustering behavior among *N. reclivata* individuals. Using the first 32 trials (each observation was considered a trial), we calculated the average number of individuals ± the standard deviation in each cluster. On average, between 3.1 and 9.0 of snails out of every group of 15 formed clusters. In other words, between 20.7% and 60.0% of snails joined a cluster. This is consistent with a random behavior in a binomial system; i.e., there is a 50:50 chance of clustering or not.

In the experimental groups, we expected to see clustering fractions proportional to the amount of individuals of certain colors. For example, with 10 purple individuals and 5 orange individuals, we would expect 2/3 (67%) of clustering individuals to be purple and 1/3 (33%) to be orange if the snails were behaving randomly. Any behaviors that exceeded or fell below these percentages at a significant level indicate departures from random behavior. For experimental groups, we determined the probability (*P*-values) that observed clusterings could have happened by chance using binomial statistics

Snails tended to cluster more significantly when they were in the minority group. In phase 2 of Batch 1, clusters contained an excess amount of orange individuals, in 4 out of 7 regions, on average (Table 2). In

Table 3. Batch 1 experimental Phases 2-7 where green snails (*Neritina reclivata*) accounted for 1/3 of the population. Columns 3 and 6 show the number of instances in which statistically significant clusters formed, and the total number of snails of colors 1 and 2 that were part of each cluster group in the following format: number of significant clusters (number of majority color: number of minority color). The *P*-values in Columns 4 and 7 indicate the likelihood of these results happening by chance.

Phase	Color 1 (10 individuals)	Color 1 excess	*P*-value 1	Color 2 (5 individuals)	Color 2 excess	*P*-value 2
2	Orange	2 (10:0), (2:0)	$7.71*10^{-3}$	Green 1-5	3 (17:5), (5:0), (5:5)	$1.51*10^{-8}$
3	Purple	1 (18:0)	$6.77*10^{-4}$	Green 1-5	5 (10:5), (10:8), (6:3), (2:2), (2:2)	$5.80*10^{-7}$
4	Orange	2 (9:1), (4:0)	0.02	Green 6-10	3 (11:16), (7:6), (5:5)	$1.10*10^{-3}$
5	Purple	0	1	Green 6-10	2 (3:4), (3:5)	0.02
6	Orange	2 (19:0)	$2.00*10^{-4}$	Green 11-15	2 (36:5), (2:0)	$7.31*10^{-14}$
7	Purple	1 (24:2)	$2.15*10^{-3}$	Green 11-15	2 (20:2), (2:0)	$3.27*10^{-9}$

Table 4. Batch 1 experimental Phases 2-7 where purple snails (*Neritina reclivata*) accounted for 1/3 of the population. Columns 3 and 6 show the number of instances in which statistically significant clusters formed, and the total number of snails of colors 1 and 2 that were part of each cluster group in the following format: number of significant clusters (number of majority color: number of minority color). The *P*-values in Columns 4 and 7 indicate the likelihood of these results happening by chance.

Phase	Color 1 (10 individuals)	Color 1 excess	*P*-value 1	Color 2 (5 individuals)	Color 2 excess	*P*-value 2
2	Green	3 (42:0), (5:0), (4:0)	$1.05*10^{-9}$	Purple 1-5	2 (13:0), (2:0)	$6.97*10^{-8}$
3	Orange	2 (17:0), (6:0)	$8.91*10^{-5}$	Purple 1-5	2 (12:6), (10:1)	$3.81*10^{-7}$
4	Green	3 (17:4), (14:2), (13:0)	$1.76*10^{-5}$	Purple 6-10	2 (6:6), (2:1)	0.02
5	Orange	4 (76:5), (2:0), (2:0), (2:0)	$1.62*10^{-3}$	Purple 6-10	2 (19:7), (7:1)	$8.08*10^{-8}$
6	Green	3 (10:2), (2:0), (2:0)	0.03	Purple 11-15	0	1
7	Orange	2 (27:0), (8:0)	$6.87*10^{-7}$	Purple 11-15	1 (29:0)	$1.46*10^{-14}$

Table 5. Batch 1 experimental Phases 2-7 where orange snails (*Neritina reclivata*) accounted for 1/3 of the population. Columns 3 and 6 show the number of instances in which statistically significant clusters formed, and the total number of snails of colors 1 and 2 that were part of each cluster group in the following format: number of significant clusters (number of majority color: number of minority color). The *P*-values in Columns 4 and 7 indicate the likelihood of these results happening by chance.

Phase	Color 1 (10 individuals)	Color 1 excess	*P*-value 1	Color 2 (5 individuals)	Color 2 excess	*P*-value 2
2	Purple	1 (3:0)	0.30	Orange 1-5	1 (3:1)	0.10
3	Green	3 (19:0), (4:0), (6:0)	$7.82*10^{-6}$	Orange1-5	1 (6:8)	0.16
4	Purple	2 (9:1), (2:0)	0.04	Orange 6-10	3 (13:12), (4:2), (5:6)	$3.45*10^{-4}$
5	Green	0	1	Orange 6-10	3 (11:5), (8:2), (2:2)	$2.9*10^{-6}$
6	Purple	2 (11:0), (10:0)	$2.00*10^{-4}$	Orange 11-15	1 (9:10)	0.08
7	Green	2 (6:0), (2:0)	0.04	Orange 11-15	1 (4:2)	0.08

Table 6. Batch 1 experimental Phases 2-7 where green snails (*Neritina reclivata*) accounted for 1/3 of the population. Columns 3 and 6 show the number of instances in which statistically significant clusters formed, and the total number of snails of colors 1 and 2 that were part of each cluster group in the following format: number of significant clusters (number of majority color: number of minority color). The *P*-values in Columns 4 and 7 indicate the likelihood of these results happening by chance.

Phase	Color 1 (10 individuals)	Color 1 excess	*P*-value 1	Color 2 (5 individuals)	Color 2 excess	*P*-value 2
2	Orange	1 (16:5)	0.13	Green 1-5	3 (17:23), (2:2), (2:2)	$5.37*10^{-3}$
3	Purple	2 (9:3), (5:1)	0.06	Green 1-5	1 (13:2)	$2.93*10^{-5}$
4	Orange	1 (20:5)	0.07	Green 6-10	2 (9:14), (3:0)	$5.26*10^{-3}$
5	Purple	0	1	Green 6-10	3 (10:14), (7:10), (4:4)	$2.99*10^{-3}$
6	Orange	2 (20:2), (2:0)	$3.43*10^{-3}$	Green 11-15	3 (10:9), (8:2), (2:0)	$1.38*10^{-5}$
7	Purple	0	1	Green 11-15	2 (9:1), (2:0)	$3.76*10^{-5}$

Batch 1, the most significant trends are associated with green individuals. Although each experiment showed excess numbers of individuals clustering, green individuals formed clusters most often. For example, out of the multiple trials during phases 2 and 4, in which green individuals were the minority in the experimental tanks, 3 out of 7 areas had a statistically significant excess of green snails. Additionally, phase 3 showed a statistically significant excess of green snails in 5 out of 7 regions (Table 3). With the *P*-value being extremely low in these cases (5.80×10^{-7}), the probability that these cluster patterns formed by chance is highly unlikely. Similarly, in phases 2-5 of Batch 1 when purple individuals were the minority, 2 out of 7 regions contained an excess amount of purple snails (Table 4).

Batch 2 snails showed similar clustering behaviors to those of Batch 1 snails. In Phases 4 and 5 where orange were the minority, 3 out of 7 areas had a significant excess of orange snails (Table 5). When green snails were the minority in Batch 2, 3 out of 7 areas contained excess green individuals (Table 6). In Phase 5 (10 orange and 5 purple), 3 out of 7 regions had excess purple individuals in them, and 0 out of 7 had excess orange individuals (Table 7).

Random behavior was only observed in snails that were part of the majority, with the exception of purple individuals in phase 6 of Batch 1 (Table 4). For example, Phases 2, 4, and 5 in Batch 1 all showed no clustering among the majority colored snails (Table 3); the same can be seen in results from Batch 2 in Phases 5 and 7 where green individuals were the minority (Table 6)

DISCUSSION

We found a significant relationship between the amount of like-colored individuals and the formations of clusters, which supports possible individual recognition in the olive snail *N. reclivata*. Overall, there were 120 total areas with significant clustering, 50 (42%) majority areas and 70 (58%) minority areas. Thirty-seven (74%) of the 50 majority areas only contained majority snails (homogeneous clustering) compared to 19 (27%) of the 70 minority areas.

These results show that individuals of the same color tend to form clusters with one another, especially when they were out-

Table 7. Batch 1 experimental Phases 2-7 where purple snails (*Neritina reclivata*) accounted for 1/3 of the population. Columns 3 and 6 show the number of instances in which statistically significant clusters formed, and the total number of snails of colors 1 and 2 that were part of each cluster group in the following format: number of significant clusters (number of majority color: number of minority color). The *P*-values in Columns 4 and 7 indicate the likelihood of these results happening by chance.

Phase	Color 1 (10 individuals)	Color 1 excess	*P*-value 1	Color 2 (5 individuals)	Color 2 excess	*P*-value 2
2	Green	2 (33:14), (7:1)	0.02	Purple 1-5	2 (6:4), (3:4)	0.01
3	Orange	2 (8:2), (2:0)	0.09	Purple 1-5	2 (7:1), (4:0)	$3.01*10^{-5}$
4	Green	2 (20:9), (2:0)	0.07	Purple 6-10	1 (13:9)	0.01
5	Orange	0	1	Purple 6-10	3 (18:6), (8:12), (3:1)	$4.46*10^{-7}$
6	Green	0	1	Purple 11-15	2 (12:5), (6:6)	$1.71*10^{-4}$
7	Orange	2 (4:0), (4:0)	0.04	Purple 11-15	1 (16:0)	$2.32*10^{-8}$

numbered by unfamiliar individuals: i.e., 70 minority clustering areas vs. 50 majority clustering areas. This is not to say that snails will not form clusters with novel individuals, but clusters that contained both colors of snails tended to have a larger amount of the minority color present. Given the fraction of the majority color compared to the minority color in any given experimental phase, these behaviors are significantly different than what is expected from random behavior.

Future studies should consider alternative placement of the experimental snails in new territories and examine the movement of individual snails once they are placed in those new territories. In all, 1341 individuals formed clusters: 584 green, 413 orange, and 344 purple. It would be interesting to examine the role of visual mechanisms involved in the clustering behavior of these snails. It may be possible that green individuals were more attracted to each other because the color green is a sign stimulus for the main food source of these snails, algae. Another possibility may be the differences in luster and clarity of the green, orange, and purple paints. Introduction to new environments may be something to consider. Although we were careful to create uniform environments for each group, there may have been cues (olfactory or otherwise) that we were unable to control. According to Prokopy and Roitberg (2001), the payoff to the individual for aggregating with or leaving groups of conspecifics depends on (a) the response of conspecifics to such actions and (b) the physiological and ecological context within which such decisions are made.

Aggregating in clusters has many mutual advantages such as increased feeding efficiencies (Focardi et al., 1985). In the sea slug genus *Aplysia*, clustering promotes reproduction (Kupfermann and Carew, 1974), and the jellyfish, *Linuche unguiculata*, significantly increases its reproductive success by social swarming (Larson, 1992). Clustering can also provide a particularly strong defense against predators, if a snail can secure an internal position within a cluster (Chase et al., 1980). In addition, forming clusters prevents desiccation by decreasing the total surface-to-volume ratio and thus reducing net evaporation (Chase et al., 1980). Moisture is conserved in this manner in aggregations of *Clypeomorus* sea snails (Moulton, 1962). Fraenkel (1968) found a direct correlation between heat resistance of intertidal mollusks and their position in the tidal zone. During observational periods, we occasionally noticed some individual snails completely above the surface of the water; if grouping is related to heat resistance or moisture conservation, in might be interesting to examine body size in relation to cluster formation in *N. reclivata*.

In the terrestrial snail *Achatina fulica*, degree of aggregation is related to the snails' ages, genetic relationships, and time of day (Chase et al., 1980). Clustering was greater when the sample population consisted of snails that hatched from one clutch of eggs compared to when they hatched from two clutches. Recently hatched snails aggregated less than older animals, and aggregation was greater during the night. The proximate basis for clustering is thought to be olfactory. Since snails often distribute themselves nonrandomly, it is reasonable to conclude that aggregation is a social behavior, although the adaptive significance does not seem to be the same in heterospecifics (Chase et al., 1980).

Recognition in invertebrates is not uncommon; there are numerous species of invertebrates that can recognize predators and learn to avoid them. For example, the sweat bee *Lasioglossum umbripenne* exhibits evasive behaviors to their ant predators, *Ectatomima ruidum*, mainly based on visual pattern recognition and ant movement (Wcislo and Schatz, 2003). Bee behavior differed based on whether an ant near the nest entrance was dead or alive (Wcislo and Schatz, 2003). Bluebell tunicate larvae (*Clavelina moluccensis*) siblings clump with other siblings that are already settled while non-siblings settle randomly (Davis and Campbell, 1996), thus exhibiting a form of kin recognition. Although we demonstrated individual recognition through clustering, we do not know whether our snails were related or not. Therefore, kin recognition in *N. reclivata* should be considered in future studies.

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