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A system for the experimental study of emigration in house mice

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A SYSTEM FOR THE EXPERIMENTAL STUDY OF EMIGRATION IN HOUSE MICE

by

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ABSTRACT

I designed and tested experimental enclosures with 1-way exits for the study of emigration in house mice. Rapid emigration from barren enclosures supported the contention that all mice can find and use the exits if conditions in the enclosures are unsuitable for them. Invariable residency in resource-rich enclosures during the spring, summer and fall revealed that resident animals will not cross the exits during routine behaviors. The enclosures and exits permitted normal emigratory and residency behavior. In experiments on the role of emigration in population regulation, the number of resident mice was consistent in enclosures with fixed levels of resources. The number of residents was about double in enclosures with twice the resources. The first male and few females added in each trial usually became resident, and mice added subsequently usually emigrated. My data suggest that mice were regulating their numbers to available resources through spacing and emigration.

PART 1. TESTING EXIT DESIGN

INTRODUCTION

Recent evidence has prompted ecologists to consider emigration as an important demographic parameter in many animal populations (Lidicker 1975, Cockburn 1988). Emigration facilitates gene flow and may lead to colonization of newly available or formerly occupied habitat. Emigration also has been implicated as an important mechanism in the regulation of at least some populations of mobile animals (Strecker and Emlen 1953, Chitty 1967, Krebs et al. 1969, Abramsky and Tracy 1979, Menke 1983, Howard 1986, McMahon and Tash 1988).

Although the potential importance of emigration in population dynamics has been acknowledged, understanding of the phenomenon is limited and disagreement persists over the stimulus for, and functions of, emigration. Progress in revealing the nature of emigration has been sluggish due to the difficulties in measuring emigration and in isolating the environmental and social conditions which may trigger the behavior (Lidicker 1975).

Though knowledge of the process of emigration is incomplete, it is often a focal point in wildlife management plans and theory. Emigration plays an important role in the theory of island biogeography, and must be considered when

managing metapopulations and designing nature preserves (Diamond 1975, Simberloff 1982, Gilpin 1987, Murphy et al. 1990). Studies that lead to a better understanding of what triggers, and interferes with, emigration are needed to direct preserve design and management decisions. For example, the effects of human altered landscapes on animal species movements are often unknown. Emigration may be inhibited by fragmented or variegated environments, resulting in reduced recolonization rates and potentially overpopulation and habitat destruction (McIntyre and Barrett 1992). Furthermore, if animals are needed for captive breeding purposes, or for reintroductions into unoccupied habitats, it may be judicious to use emigrants, which otherwise would have low survival rates, rather than deplete the resident population. While unconstrained emigration is often necessary to meet management goals, it is sometimes important to keep a population limited to certain areas to prevent disturbance elsewhere, such as when managing exotic fishes or commensal rodents. Attempts to keep species localized will inevitably fail if expected barriers are ineffectual. Testing various habitat features with a systematic method may quickly find the factor most likely to act as a true barrier, or it may prove that no barriers can be counted on to completely prevent expansion. These few examples illustrate that a greater understanding of

emigration is vital if wildlife managers are to make proper decisions.

Several techniques have been used to study emigration in the field, including radio telemetry (Hilborn and Krebs 1976, Wolff and Holleman 1978), removal grids (Gaines et al. 1979, Baird and Birney 1982), and enclosures with exits or emigration traps (Tamarin et al. 1984, Verner and Getz 1985, Johnson and Gaines 1987). Results from these and similar studies, though valuable, were inconclusive because environmental conditions could not be controlled sufficiently and, more importantly, residents, emigrants, and mortalities were not adequately identified and enumerated (Lidicker 1975, Gaines and McCleneghan 1980, Cockburn 1988, Matter et al. 1989).

Studying emigration in a laboratory setting would allow greater control of environmental conditions and non-emigratory losses. If the setting permits normal emigratory behavior, it would also make possible the identification and enumeration of all residents and emigrants (Matter et al. 1989). Laboratory experiments using exits that allow movement out of an enclosure have been used to study the relation between social behavior, resource availability, and emigration in several animals (Chapman 1962, Slaney and Northcote 1974, Butler 1980, Wilzbach 1985). Individuals that moved through the exits were considered emigrants, and

those that remained in the enclosure were considered residents. The experimental designs in these studies were not tested, however, to ensure that: 1) all animals could find and use the exits, or that emigration was not inhibited and 2) animals that traversed the exits were emigrators and not residents which passed through the exits during routine exploratory movements (Matter et al. 1989).

Matter et al. (1989) proposed a rationale for designing and testing laboratory settings open to emigration, and demonstrated systems using bluegill (*Lepomis macrochirus*) and crayfish (*Orconectes causeyi*). They maintained that the exits should incorporate a negative feature to assure that only individuals highly motivated to leave the system would use them. The bluegill in their experiments, for example, had to swim through a v-shaped notch in very shallow water to leave the enclosure. Tamarin et al. (1984) utilized a similar rationale for identifying emigrants in a field enclosure by requiring them to travel across a relatively large area of non-habitat, a behavior which residents were unlikely to exhibit.

Butler (1980) studied the relation between population size, social behavior, and emigration of house mice (*Mus musculus*) in laboratory enclosures with controlled environmental conditions and exits that required emigrants to cross water-filled troughs. Animals were placed in

enclosures with the exits closed and observed to identify dominant and subordinate individuals. The exits were opened after 10 days. Ninety-seven percent of the mice which crossed the exits during the following 5 days were subordinate individuals. A relatively consistent number of mice remained in the enclosures. These results suggest that the exits prevented the inadvertent loss of residents (dominants) but allowed emigration of subordinates. However, Butler (1980) did not test the exits to ensure that all mice could use the exits, and that only emigrants would cross the water-trough.

The purpose of my project was to design and test an experimental system for the study of emigration in house mice. The tests of the system were devised to ascertain: 1) if all individuals are able to find and use the exits, and (2) whether individuals that traverse the exits are emigrators, or residents that cross during routine exploratory behavior.

METHODS

I conducted this study at the Arizona Cooperative Fisheries and Wildlife Research Unit compound, West Campus Agricultural Center, 3199 North Freeway, Tucson, Arizona.

Study Animals

I used wild-caught house mice in all experiments. I

captured the mice within the Tucson area at 3 equine boarding stables and the Arizona Cooperative Research Unit compounds at North Freeway and Campbell Avenues. Each animal was ear-tagged (National Band and Tag Co., Model 1005-1) and held separately in aquaria inside a cooled building at the study site for up to 10 days prior to use. I provided each aquarium with sand, rocks, twigs, a cardboard juice can with cotton for nesting, and a filled water bottle. Food was scattered liberally on the sand substrate. I flushed the aquaria, water bottles, rocks, and twigs with water, and replaced nest cans, cotton, sand, and food between individuals. Visibly pregnant or lactating females and sick individuals were not used. Males were used regardless of sexual condition (testes scrotal or abdominal). The minimum weight of mice used was 10 g, but 25 of 28 were $\geq$ 13 g. Each individual was used in one trial and then released.

In preliminary trials, individuals of both sexes left a resource-rich setting within 2-3 nights after being introduced singly, but occupied the enclosure for 7 nights when introduced together. These results indicated that the presence of a conspecific (probably the opposite sex) was necessary for a residency response in the enclosures, and mice were added as male-female pairs in all subsequent trials.

Enclosures

All experiments were conducted in 2, 5.5-meter diameter circular enclosures with 1-meter high corrugated steel walls (Doughboy above-ground swimming pools). The enclosures were kept clear of vegetation and lined with quarter inch hardware-cloth to prevent escape or entry by burrowing through the soil. The hardware-cloth was covered with about 3 cm of sand and gravel. I covered both enclosures with 50% shade-cloth to provide shade, prevent predation by feral cats, raptors and roadrunners, and prohibit entry by squirrels which occupied the compound.

Exits

I equipped each enclosure with 1 exit, patterned after the water barriers used by Butler (1980). The exits consisted of a 10 cm X 20 cm opening at the base of the enclosure wall with a pan of water immediately outside the opening. The pan was 45 cm long, 18 cm wide, and 13 cm deep and was filled with about 11 cm of water. Hardware-cloth ramps lead into and out of the water pans at either end. A panel angled down from the top of the doorway to about 2 cm above the pan's rim forced mice to enter, and not simply jump over, the water. Clear plexiglass walls extended from the inside-bottom of the pan to 20 cm above the pan to prevent escape.

After an individual traversed the water barrier, it

entered a 36 cm X 105 cm hardware-cloth chamber containing 4 aluminum live-traps. The traps were unbaited, but cotton was placed inside during the winter months. The trap-chamber had a plywood floor with ¼-inch hardware-cloth walls and top. The wall facing the enclosure was made of plywood to block sight of the traps which may have been attractive as shelter sites. I kept the exit as visually open as possible (e.g., using plexiglass and hardware-cloth) so as not to create a tunnel-like or darkened area. The exit and trap-chamber were designed to be as non-attractive as possible to help ensure that animals were not drawn through the exit, and that departures were a consequence of conditions within the enclosure. The floor of the trap-chamber at the end of the moat was lightly dusted with flour to determine, by the presence of tracks, if animals crossed the moat but returned to the enclosure without entering a trap.

Three Step Test of Exits

I utilized a 3-step test to determine if the exits would permit normal emigratory and residency responses. First, 1 male and 1 female mouse were introduced into a "barren" enclosure with no food or shelter present. I anticipated that the lack of resources would stimulate the mice to leave the barren enclosure relatively quickly, if all mice are able to find and use the exits.

In step 2, each pair of mice was introduced into a

"resource" enclosure within 1 day of leaving the barren enclosure. Excess food (1 part commercial mouse/rat food, 1 part rolled oats) and water were provided at 5 stations established at the center and around the perimeter of the enclosure. Food dishes were covered to keep food dry. Shelter/nest sites consisted of 4 underground nest boxes and 4 above-ground "condos" distributed throughout the enclosure. Each subterranean nest box was a 5.7-liter ("6-pack") beverage cooler buried with the lid at ground level for easy access. A pvc pipe leading from the surface down through a hole cut in the side of the cooler served as the entrance. The entire unit was covered by a 61 cm X 152.5 cm plywood board on 20 cm legs to provide shade and additional cover. Condos were plywood boxes measuring 46 cm tall, 30 cm deep, and 78.5 cm wide, divided into 4 levels with plywood shelves. I placed a sheet of styrofoam on the sand/gravel floor to serve as insulation from cold and moisture. I covered the condos with large plastic trash bags during the winter to provide additional insulation and protection from rain. Cotton and hay were placed in all shelters. Eight pvc pipe elbows and t's were distributed in the enclosure for added complexity and cover.

Animals that stayed in the resource enclosure for 7 nights and did not cross the exit were assumed to have taken up residency. I chose 7 nights as the criterion for

residency based on the short length of time expected for an emigration response if conditions were unsuitable, and on the rapid emigrations of mice in preliminary trials.

Finally, individuals which took up residency in the resource enclosure were trapped out and reintroduced into the barren enclosure, step 3. If a second rapid emigration occured, I assumed that their initial experience through the exit was not so negative as to preclude further emigration, and that residents in the resource enclosure were exhibiting volitional residency.

This 3-step test was conducted with 14 pairs of mice. All mice were introduced into enclosures within 15 minutes of sundown. I did not begin new trials during storms, but rain did occur in the midst of some trials. To limit stress during introductions, mice were removed from aquaria and placed in the enclosures while still inside their nest cans. The nest cans were removed after 5 minutes. I blocked the exits with hardware-cloth until 15 minutes after introductions to stop animals from crossing the exit during initial fright responses.

RESULTS

Step 1 - Barren Enclosure

Every pair of mice left the barren enclosure during the first night, many within 1 hour (Table 1).

Table 1. Number of hours (after exits were opened) that mice stayed in the 2 barren enclosures, the date they were added to the resource enclosure and the number of the night after introduction in which mice either emigrated from (<7), or were trapped out of (>7), the resource enclosure.

Pair Number		BARREN 1 Hours	RESOURCE Date	RESOURCE Nights	BARREN 2 Hours
1	♂	0.2	9/25	8	<12.0
	♀	0.2		8	<12.0
2	♂	<12.0	10/9	8	<12.0
	♀	<12.0		8	<12.0
3	♂	0.75	11/6	8	<12.0
	♀	0.75		8	<12.0
4	♂	4.5	11/16	11	<4.0
	♀	4.5		8	<4.0
5	♂	0.2	11/29	<1	
	♀	0.2		<1	
6	♂	3.5	12/8	<2	
	♀	3.5		8	0.2
7	♂	1.5	1/1	<1	
	♀	1.5		<2	
8	♂	0.2	1/14	<1	
	♀	0.75		<3	
9	♂	1.0	2/14	<1	
	♀	1.0		<2	

Table 1 continued.

Pair Number	BARREN 1 Hours	RESOURCE Date	RESOURCE Nights	BARREN 2 Hours
10 ♂	0.75	3/4	8	2.5
♀	0.75		8	2.5
11 ♂	1.5	3/17	10	0.4
♀	1.5		12	0.4
12 ♂	0.4	4/4	10	<1.0
♀	0.4		8	0.4
13 ♂	0.6	5/1	8	<1.0
♀	0.6		8	<1.0
14 ♂	<1.0	5/21	21	*continued
♀	0.75		14	to Part 2

Step 2 - Resource Enclosure

Nine of the 14 pairs and the female of pair #6 remained in the resource enclosure for more than 7 nights. The 9 pairs which took up residency were introduced between March and mid-November. The 4 pairs and male #6 which left the resource enclosure in less than 7 nights were introduced between 29 November and 14 February. None of the mice crossed the exit, avoided the traps and returned to the enclosure.

Step 3 - Barren Enclosure

Every pair, and female #6, that stayed more than 7 nights in the resource enclosure left within 1 night after being re-introduced into the barren enclosure.

DISCUSSION

The consistent behavior of mice when placed in the first and second barren enclosures leaves little doubt that they can rapidly find and use the exits, if motivated to do so, and that passing through the exit once did not prevent them from traversing it again. It follows that "residents" in the resource enclosure were able to leave, and were not simply fenced in by their previous experience with the exit.

The results from the resource enclosure suggest that the resources I provided were adequate to promote residency of house mice during March through mid-November, but were

inadequate during the winter. Other studies have revealed that movements out of fields and into structures during October and November are a common phenomenon in house mice (Fenyuk 1941, Rowe et al. 1963, DeLong 1967, Lidicker 1975, Bronson 1979, Stickel 1979). Feral mice resided in the unheated building housing the aquaria on the Research Unit compound and were active throughout the winter. My outdoor enclosures apparently were not adequate to counteract the impulse for fall migration to a more structured or protected environment. The fact that female #6 resided in the enclosure with no apparent ill-effect may mean, however, that the resources I provided were nearly sufficient to satisfy the winter requirements for residency of house mice in general. This problem clearly must be dealt with before using outdoor enclosures for long-term, year-round experiments on emigration and population dynamics in house mice.

The consistent residency of pairs in the resource enclosure during much of the year, in light of the rapid departures during winter, suggests that the exits reduced the likelihood that animals would cross the exit during routine exploratory behavior, if they were motivated to stay in the enclosure.

7-Day Residency Assumption

The 7-day criterion I used for designating residency

was substantiated by the results. Of the 58 emigrations that took place during this testing, 54 occured the first night after introduction, 3 occured the second night, and 1 occured the third night. No mice left the enclosures after the third night. In 2 trials described later in this thesis, residents stayed in the enclosures for up to 42 days. It is clear that the initial "decision" to reside in or leave the enclosures was made well before the seventh day after introduction.

PART 2. POPULATION REGULATION EXPERIMENTS

INTRODUCTION

Populations do not increase without limit, despite their potential to do so (Krebs 1972), but controversy remains over the mechanisms responsible for preventing unlimited increase. Proposed extrinsic regulating factors include weather, disease, predation, and food supply (see reviews in Chitty 1960, Krebs and Myers 1974, Lidicker 1978, Krebs 1984). Self-regulation hypotheses assert that species have evolved internal mechanisms with which to regulate their own densities, without requiring external factors to do so. Social stress (Christian 1975, 1978, 1980), genetic-polymorphic behavior (Chitty 1960, 1967) and other self-regulation hypotheses are reviewed by Krebs (1978), Gaines and McClenaghan (1980), and Cockburn (1988).

Spacing behavior can play an important role in self-regulation because it leads to a division of resources (Lomnicki 1978). Individuals which cannot claim a space or territory must emigrate due to inaccessability of resources and possibly increased aggression from conspecifics. Recent studies have supported the idea that spacing and emigration can regulate at least some populations of mobile animals (Bianchi 1984, Wilzbach 1985, McMahon and Tash 1988). Experiments preventing normal emigratory responses provide

further evidence that emigration plays a key role in the population dynamics of some, and probably many, species (Strecker and Emlen 1953, Krebs et al. 1969, Gaines and McCleneghan 1980, Lidicker and Caldwell 1982, Johnson and Gaines 1987).

Most of the interest in, and research on, emigration and population regulation has been focused on small mammals, but clear evidence that spacing and emigration alone are sufficient to regulate populations has not yet been offered. Some authors have maintained that the number of emigrations they observed were not sufficient to restrict population increase (Dunford 1977, Tamarin et al. 1984, Verner and Getz 1985). The greatest impediment to determining the importance of emigration in regulation has been the inability to both operationally identify and enumerate emigrators and residents, and control environmental factors that may have a bearing on the mechanism (ie. predation).

In Part 1, I described an experimental design for the study of emigration in house mice, and tests which revealed that the system at least partly solves these problems. I used the same design to test the hypothesis that house mice would regulate their numbers to available resources through spacing and emigration. Hence the population in a system with 2X resources and space should be roughly twice as large as that in a similar system with X resources and space.

House mice are strongly territorial, usually with 1 male and several females (2-10) defending an exclusive area (Bronson 1959, Crowcroft and Rowe 1963). I anticipated that, as pairs were added to the enclosures, males would begin emigrating as available territories became occupied. I expected females to begin leaving sometime later. I predicted that 1-5 males and 6-12 females would reside in each enclosure.

METHODS

Study animals

Methods to capture and handle house mice were as described in Part 1. Thirty-five of 47 males used in all trials had testes scrotal. Forty-two of 47 females used were non-lactating and 5 were pre-/post-lactating. Lactating or obviously pregnant females were not used. Weight was recorded at the time of capture.

Enclosures

Study area, enclosures, and exits were as described in Part 1 except that the 2 enclosures were supplied with the same resources, the subterranean nest boxes used in Part 1 were eliminated, and complexity was increased by adding more plywood structures of varying size to each enclosure. For the ensuing experiments, I supplied each enclosure with the following resources: 2 "condos" (described in Part 1); 2

double boxes (30 cm wide X 61 cm long X 9 cm tall on top of 30 cm wide X 61 cm long X 15 cm tall); 1 single box (30 cm wide X 61 cm long X 15 cm tall); 4 half boxes (30 cm wide X 30 cm long X 10 cm tall); 2 half boxes under plywood covers (61 cm X 152.5 cm on 20 cm legs) with burlap sacks covering 40-60% of the entire unit; 1 cinder block covered with burlap; 5 food and water stations; 6 PVC elbows or t's at random locations (Figure 1).

Each plywood structure had 2-4 small entrance holes and a styrofoam floor to insulate from cold and moisture. A handfull each of hay and cotton were placed in each structure (on the first 2 floors of multi-leveled structures). About 42.5 g of food was also provided in a small cup in each structure at the beginning of a run. Food and water stations were kept well stocked.

In order to compare population sizes between 2 resource levels, I connected the two enclosures with an enclosed plywood runway (10 cm wide X 20 cm high X 160 cm long). By blocking or unblocking the runway I was able to conduct trials in both single-, and double-enclosure systems. Thus, I could compare the number and identity of residents and emigrants in "single" trials to those in "double" trials with twice the available resources and space.

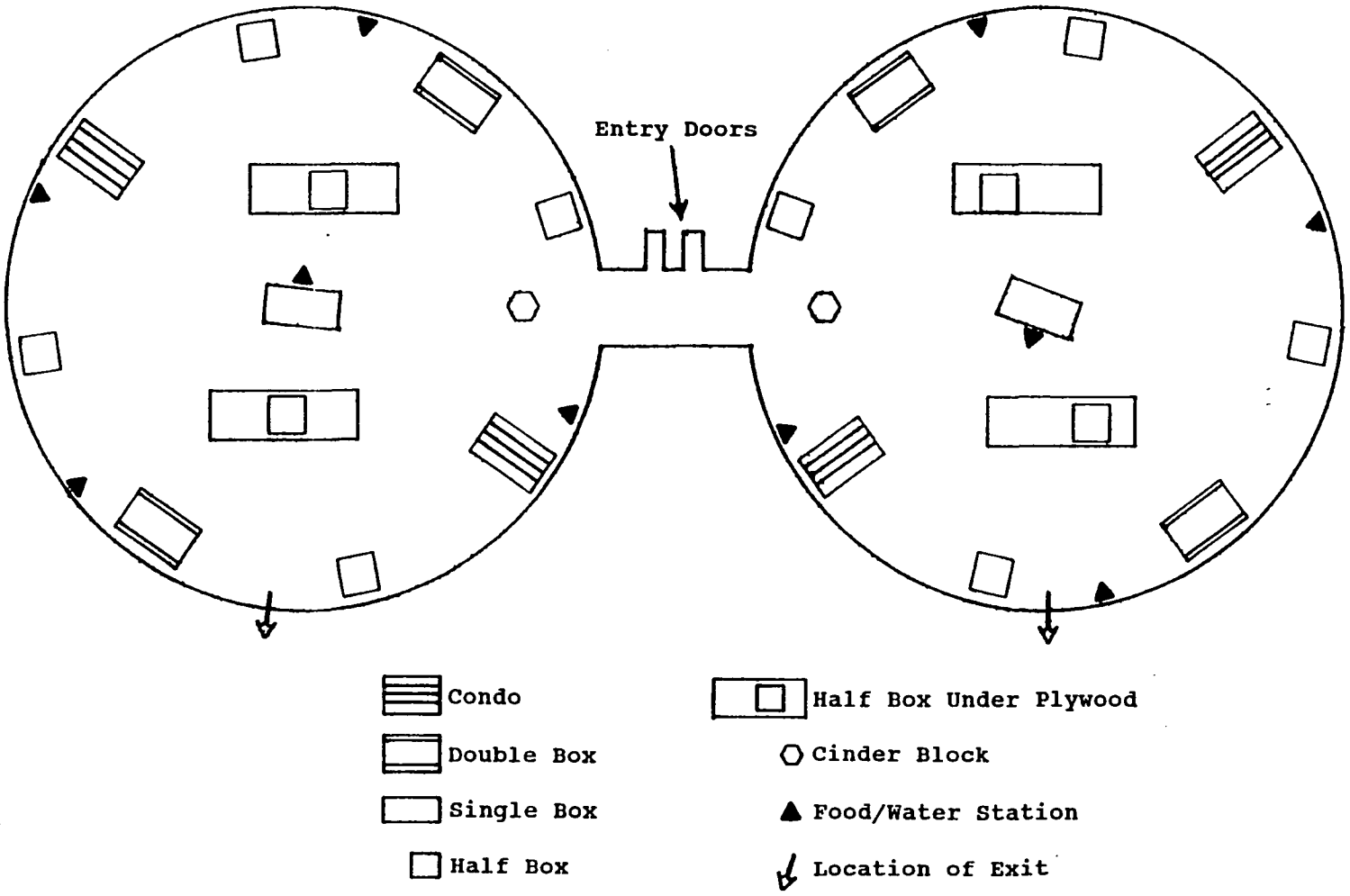

Figure 1. Configuration of enclosures and resources for regulation experiments.

Introductions

A male-female pair of house mice was introduced to a single or double enclosure every 2 days or as soon as new mice could be acquired. New pairs were added to enclosures until 3 consecutive pairs emigrated, though not necessarily in the order added. The length of time between introductions was based on the times required to emigrate as determined in Part 1, when all but 1 emigration took place in 1 or 2 days.

Pairs were introduced in single trials as in Part 1. In double trials mice were introduced, again while still inside their nest cans, through 2 doors in the middle of the runway (Figure 1). In this way, I did not influence into which enclosure the mice entered.

RESULTS

I have completed 4 single-enclosure trials and 2 double-enclosure trials. It is important to note that the first 2 single-enclosure runs were conducted at the resource levels described in Part 1 (4 condos, 4 subterranean boxes, 8 pvc units, 5 food and water stations). These trials may not be used in the final analysis but are included here to assist in the development of ideas and preliminary discussion.

The number of males and females remaining at the end of

the 4 single-enclosure trials was fairly constant (Table 2), despite the difference in resource levels. One male held the entire enclosure as his exclusive territory in 3 of the 4 trials. The fourth single-enclosure trial had no males at completion because the 10-day resident male departed the enclosure on the last evening of the trial (perhaps in pursuit of the introduced male). Two females remained in 3 of the single-enclosure trials and 3 remained in the fourth. Total number of mice ranged from 2 to 4.

A single male was able to exclusively claim both enclosures in the 2 double-enclosure trials. Five and 6 females were resident making the total population size in the double enclosures 6 and 7 animals.

Order of introduction was apparently the primary factor determining which males and females resided in the enclosures. All male residents, in both single and double trials, were the first male introduced. Lidicker (1976) found that house mice can establish territories within 1 night in areas of low substrate complexity. Agressive territorial defense by the first males introduced apparently prevented subsequent males from staying in the enclosures. Fourteen of the 18 females from the first 3 pairs added in all 6 trials were residents. Two of the 12 females in pairs 4 and 5 were resident, and 4 of the 17 females in subsequent pairs were resident.

Table 2. Number of residents at the conclusion of preliminary single-enclosure and double-enclosure regulation trials.

TRIAL		♂	♀	TOTAL
SINGLE	1	1	3	4
	2	1	2	3
	3	1	2	3
	4	0	2	2
DOUBLE	1	1	6	7
	2	1	5	6

Litters were found in both double-enclosure trials (lasting 29 and 42 days, respectively). The first trial had 2 litters of 2 and 5 juveniles. Of the 4 females without litters, 3 were pre-lactating and probably pregnant and 1 was non-lactating. Three females in the second double-enclosure trial had litters of 5, 5, and 7 young. One of the 2 remaining females was pregnant. Some of the litters were still hairless "pinkies" while others were mobile and presumably approaching subadult status.

One male was unaccounted for at the end of each double-enclosure trial. A total of 4 males and 1 female were found dead during or at the end of double-enclosure trials. Two were found lying in the open, with tail and flank wounds visible, and 3 were inside nest structures, often decomposed under sand piles. No fatalities occured during single-enclosure trials.

DISCUSSION

Regulation

The data thus far indicate that the numbers of house mice were regulated to the available resources in the enclosures. The number of individuals residing in the single- and double-enclosure trials was fairly consistent, and was about twice as large in the double enclosures as in

the single enclosures.

Mortality attributable to extrinsic factors was eliminated (predation, food limitation), or monitored (disease, weather), and did not play a significant role in regulating house mouse numbers in my enclosures. The number of residents in the single enclosures was consistent, despite the increase in shelters and complexity for the second 2 trials. Also, all of the available shelters were not used in any trial, indicating that shelter sites were not limiting.

The stress hypothesis asserts that densities increase until physiological responses to increased social strife increase susceptibility to disease and parasites, inhibit reproductive activity, and precipitate pathological behaviors such as cannabilism (Christian 1980). The high level of reproductive activity and litter survival in the double-enclosure trials, and the low overall mortality, indicate that stress probably did not affect the resident individuals to a great degree. The physiological and behavioral pathologies associated with the stress hypothesis are usually noted in confined populations. In this work, I mimicked what I assume is the more prevalent situation in nature - an unconfined population. It seems that when provided an outlet, territorial mice did not allow densities to increase to the point that stress would became a factor.

Because food and shelter sites were not limiting, space was presumably the critical resource to which regulation occured. Emigration was relatively continuous after the first pairs were introduced. I conclude that the data reported here, though not expansive, support my research hypothesis. The first males in the enclosures established and defended territories, with the first few females "allowed" to share the space. Mice added subsequently could not find an undefended area and emigrated. Thus spacing behavior coupled with emigration of individuals not attaining, or not being accepted into, territories was the mechanism of regulation for the house mice in the enclosures.

My work essentially mimicked colonization of newly opened habitat followed by continuous immigration. Strong territorial behavior, demic structure and stability of family groups have been observed in some populations of house mice (DeLong 1967, Berry 1970, Bronson 1979). Agressiveness toward strangers by a family group is usually rapid and extreme (Crowcroft and Rowe 1963). In enclosed populations, Lidicker (1976) achieved very high densities of house mice through recruitment of young, but immigrants were harrassed almost continuously until they died. He found that territoriality in house mice limits the number of, but not size, of social groups, and hence not the ultimate size of

the population. With this social strategy, it may be necessary to allow life history cycling within the enclosures in order to understand how spacing and emigration are utilized by house mice during increases in population size through recruitment of young as well as immigration.

Implications on the system

The level of reproductive activity and litter survival in the double-enclosures is encouraging because lack of reproduction and mortality or abandonment of young may have indicated "fence effects", pathological responses to overcrowding in confined areas (Lidicker 1976, Boonstra and Krebs 1977). It is evident that the enclosure and exit system that I used allowed normal functioning of house mouse social behavior. The lack of young being born in the single trials was likely due to rapid completion times (9-21 days) of trials.

The likelihood of escape from the enclosures increased with time, thus it would not be surprising if the 2 individuals that were not found had escaped. It is possible, however, that they died in the enclosures and were not found when the trial was completed and the enclosures were examined and cleaned. The 5 dead and 2 missing individuals were identified and enumerated, and therefore do not pose significant problems in the acceptance of this system for the study of emigration and population regulation.

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