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EXPERIMENTAL STUDY OF RESIDENCY AND EMIGRATION  
IN HOUSE MICE

By

Cameron Laurence Johnson

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A Thesis Submitted to the Faculty of the  
SCHOOL OF RENEWABLE NATURAL RESOURCES  
In Partial Fulfillment of the Requirements  
For the Degree of  
MASTER OF SCIENCE  
WITH A MAJOR IN WILDLIFE AND FISHERIES SCIENCE  
In the Graduate College  
THE UNIVERSITY OF ARIZONA

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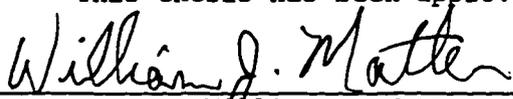
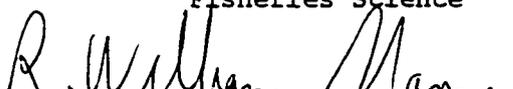
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## ABSTRACT

I used enclosures with exits for emigration to test whether house mice could regulate their numbers by emigration to two levels of resources. Exits had a water obstacle likely to be crossed only by true emigrants. Enclosures had excess food and water and the number of shelters was held constant. I introduced a pair of mice into enclosures about every other night, until no more would become residents. I ran 7 trials in single enclosures and 8 in double enclosures (2 single enclosures joined with a tunnel). The number of mice that stayed within a given size enclosure was consistent, and was 2.3 times higher in double enclosures than in single enclosures. Weather, predation, starvation, and disease did not act in any trials. My data support the contention that house mice can control their population numbers through spacing and emigration.

## INTRODUCTION

Animal populations have the ability to grow exponentially, but rarely do. The question of what regulates animal populations is controversial, and the mechanisms associated with regulation remain unclear (Murdoch 1994; Krebs 1995, 1996). Resources within the habitat of a given population set a theoretical upper limit to the number of animals that can be supported in a given area (i.e., carrying capacity, Leopold 1933). However, as a population reaches carrying capacity, the potential for reproduction is not necessarily lost. Thus explaining the fate of individuals above the carrying capacity of the habitat is a critical part of any hypothesized mechanism of population regulation. The search for regulatory mechanisms has not produced unequivocal data to support a single theory. There is disagreement about whether biologists should seek a single explanation for population regulation (Krebs et al. 1973). Recently, Holmes (1995) warned that searching for a single cause for population regulation is futile and may even hinder progress in understanding population dynamics. However, experimental tests of any proposed mechanism are needed to understand which processes are involved (Matter et al. 1989, Murdoch 1994, Krebs 1995).

There are two main schools of thought concerning population regulation in animals. One suggests that populations are regulated by extrinsic factors, such as disease (May 1983), predation (Errington 1936, Buehler and Kieth 1982), resource supply (Strecker 1954, Hansen and Batzli 1978), and weather (Andrewartha and Birch 1954). The second school believes that intrinsic factors regulate populations (Krebs et

al. 1973, Krebs 1996). Intrinsic factors refer to the ability of animals to control their own population numbers. Several mechanisms of self-regulation have been proposed including: 1) genetic polymorphism resulting in density-tolerant and density-intolerant animals (Lidicker 1962, Chitty 1967); 2) density-dependant reproductive rates, wherein reproduction declines as part of the stress response to increasing density (Brown 1953, Strecker and Emlin 1953, DeLong 1967, Christian 1971); 3) juvenile mortality due to cannibalism or parental desertion (Southwick 1955, Pennycuik and Reisner 1989); and 4) spacing and emigration (Krebs et al. 1973, Gaines and McClenaghan 1980, Krebs 1984, Tamarin et al. 1984, Luk'yanov et al. 1994).

The discovery of abnormal demography of fenced populations of mobile animals, compared to unfenced populations, is strong evidence that emigration is important in population regulation. Populations within fences quickly grow to abnormally high densities, exhibit high aggression, reduced fertility, and high mortality; features collectively referred to as "fence effects" (Krebs et al. 1969, Krebs et al. 1973, Ostfeld 1994). The role of spacing and emigratory behavior in population regulation has been studied (e.g., Strecker 1954, DeLong 1966, Krebs et al. 1973, Tamarin et al. 1984, Verner and Getz 1985) but has not been clearly demonstrated experimentally, due largely to difficulties associated with identifying and enumerating resident animals and emigrants and with controlling the experimental environment. Verner and Getz (1985) used electronic counting gates to determine the number of voles moving through a fenced enclosure, but animals leaving

the enclosure may have been simply foraging or have incidentally passed through the exit gates during exploration. Tamarin et al. (1983) classified emigrant voles as those willing to cross areas not normally inhabited, but not all emigrants or residents within fenced enclosures were counted and resources were not controlled. Also, animals taken by predators or dying from other causes inside the fence were not counted. Thus, the role of emigration in regulating the population was difficult to assess. Similarly, Malizia et al. (1995) classified fossorial rodents that moved above ground (a natural obstacle avoided by resident animals) away from areas of residency, as emigrants, but the authors failed to attain a complete count of emigrants or residents within the study population or to control resources.

Recently, Carpenter (1996) has argued that small-scale experimental manipulations lack the complexity found in nature and therefore may be of limited value in broad ecological applications. While there are certainly limitations to what can be claimed as a result of small-scale experiments, they are necessary to gain a better understanding of the fundamental processes of population dynamics as mediated through the responses of individual animals to the conditions they encounter. A better understanding of the role of spacing and emigratory behavior in population regulation can be gained in experimental settings where all animals can be counted, resources can be controlled, and no animals are lost to external forces such as predation, disease, or weather. However, the setting must allow animals

to undergo normal settling (i.e., residency) and emigration responses (Matter et al. 1989).

I examined the responses of house mice (Mus musculus) to the presence of increasing numbers of conspecifics in enclosures with a fixed level of food, cover, and water, and open to emigration through exits. The experimental enclosures I used allowed animals to respond to each other and to the environment as they would in nature, and allowed me to maintain control of environmental conditions and to monitor numbers of residents and emigrants.

I predicted that if house mice could control their own population numbers in an area through spacing behavior and emigration alone: 1) mice introduced to a resource-rich enclosure would become residents until some socially mediated limit (e.g., tolerance density, Dasmann 1964) of the enclosure was reached; 2) mice added in excess of this limit would emigrate from the enclosure; 3) the number of resident mice would be relatively consistent among trials with similar levels of resources; and 4) increasing the size of the enclosure would cause the number of residents to stabilize at a higher value. Because more than 1 female may reside in the territory of a male house mouse (Reimer and Petras 1969, Bronson 1979), I also predicted that the number of females that stayed in an enclosure would be greater than the number of males.

## METHODS

I conducted the study on the Arizona Cooperative Fisheries and Wildlife Research Unit Compound, Tucson, Arizona, between May, 1994 and October, 1995. Nelson (1992) discovered that outdoor enclosures, even with abundant food, water, and cover structures, did not trigger residency in house mice during winter (November to March), so I did not attempt trials during these months.

### Study Animals

House mice were live-trapped in 12 locations in Tucson, Arizona with Sherman live traps baited with peanut butter and oatmeal. All mice were handled in accordance with regulations set by the University of Arizona, Institutional Animal Care and Use Committee (Protocol #95-143) and with precautions against hantavirus (Mills et al. 1995). Mice were sexed, weighed, ear-tagged (National Band and Tag Co., Model 1005-1), and checked for general health. Visibly pregnant or lactating mice, sick mice, or mice weighing <10 g were not used. Males were used regardless of sexual condition (i.e., testes scrotal or abdominal). Mice were housed singly in aquaria containing food, water, wood chips, and a cardboard shelter. Food consisted of a mixture of horse feed (Arizona Feeds equine formula, Eagle Milling Co., Tucson) and rolled oats. Mice were released near the study site at the end of each trial.

### Enclosures

Experiments were conducted in circular enclosures 5.5 m in diameter, with 1-m high walls (i.e., single enclosures). Wooden tunnels were placed between pairs of enclosures to double the test area and resources (i.e., double enclosures). The enclosure floors were cleared of vegetation and lined with 1-cm mesh hardware cloth to prevent escape by mice and immigration of burrowing animals. The floor mesh was covered with sand and gravel about 3 cm deep. I covered the tops of enclosures with shade cloth (50%) to provide shade and protection from predators (e.g., feral cats, roadrunners [Geococcyx californianus] and raptors), and to prevent entry by rock squirrels (Spermophilus variegatus). I provided each enclosure with food (1100 g) equaling about 100 times the weight of a mouse at the beginning of each trial and I maintained food at this level throughout all trials to ensure an abundance of resources. Water was provided at 4 sites in each enclosure, and food was scattered liberally around the perimeter of each enclosure. Eight shelter units, each consisting of an inverted plastic tub (4, 10-L tubs and 4, 20-L tubs) were placed around the perimeter of each enclosure (Fig. 1). A sheet of 2-cm thick Styrofoam and wood shavings placed under each tub provided insulation and nesting material.

#### Exits

Exits from enclosures required that mice cross a water-filled trough to emigrate. The water trough served as an obstacle which would be crossed by emigrating individuals only. Nelson (1992) showed that mice crossed a water obstacle readily if an enclosure lacked resources,

but would not cross if food, cover, and water were provided in the enclosure. His results indicated that all mice could find and use exits (i.e., emigration was not inhibited) and that mice that traversed the exits were emigrants and not residents that passed through the exits during routine exploratory movements (Matter et al. 1989). A similar approach has been used to study emigration in pupfish (McMahon and Tash 1988) and crayfish (Menke 1983). The exits I used are similar to those designed by Butler (1980) and tested for house mice by Nelson (1992), according to the criteria set by Matter et al. (1989).

Each enclosure had 1 exit that consisted of a 10 cm X 20 cm opening at the base of the enclosure wall with a pan of water (45 cm long X 18 cm wide X 13 cm deep) immediately outside the opening. Hardware-cloth ramps lead into the water at each end of the pan. A hardware-cloth panel was angled down from the top of the doorway to about 5 cm above the water surface to force emigrating mice to enter the water, and not simply jump over it. Plexiglass walls extended 20 cm above the pans and hardware-cloth covers prevented escape. Animals that crossed the water entered a hardware cloth enclosure (36 cm X 105 cm) containing 4 unbaited Sherman traps. Cotton was placed inside each trap to insulate mice in cold weather. Traps were checked for emigrants each morning.

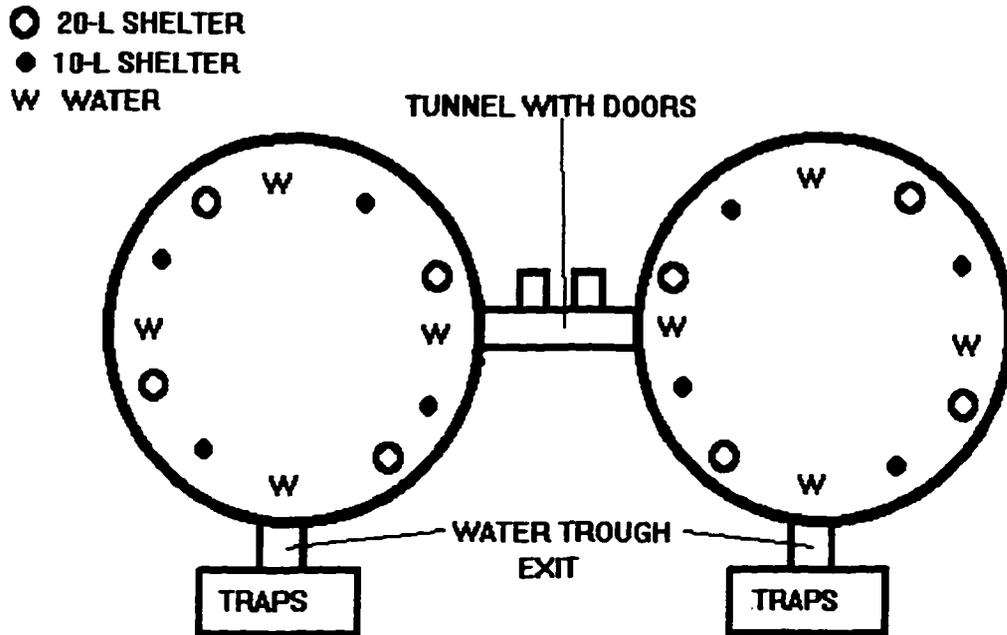


FIGURE 1. Enclosures used to study emigration and residency in house mice.

### Trials

Nelson (1992) found that mice had to be added in pairs for them to settle in experimental enclosures. Therefore, I added mice to enclosures in male-female pairs in all trials. I added mice to enclosures at a rate of about 1 pair every other night (depending on availability of test animals) until 3 successive pairs of mice emigrated from the enclosure. I arbitrarily decided that 3 successive emigrating pairs was indicative that full residency had been achieved. I added mice into enclosures within 15 minutes of sunset, a time when mice normally become active. Mice added to double enclosures were introduced through a door in the tunnel that joined 2 single enclosures (Fig. 1). Mice were placed directly into single enclosures. I left mice in cardboard shelters during the transfer from the holding aquarium to the enclosure, and I removed the shelters after mice vacated them. I blocked the exit from enclosures for 15 to 30 minutes following introduction of mice to prevent mice crossing the exit during their initial fright response. At the end of each trial, all shelters and food stations were removed and all resident mice were live-trapped and counted. I completed 7 trials with single enclosures and 8 trials with double enclosures.

### Behavioral Observations

After I introduced mice to enclosures, I observed them through small holes in the walls of the enclosures for up to 60 minutes in some

trials. I recorded the behavior of all mice I observed during these time periods.

## RESULTS

### Single Enclosure Trials

A single male and a single female became resident in each of 6 single enclosure trials; 2 females stayed in 1 trial. The majority of animals added early became residents and stayed to the end of trials. Overall, 6 (85%) of the resident males and 7 (88%) of the resident females were animals from the first 2 introductions of their respective trials. The number of mice added ranged from 4 to 7 pairs per trial. The duration of trials ranged from 8 to 18 days.

### Double Enclosure Trials

The mean number of resident males and females in double enclosure trials was 1.8 and 3.1, respectively (Table 1). Overall, 12 (86%) of the resident males and 21 (84%) of the resident females were animals from the first four introductions of their respective trials. The number of mice added ranged from 5 to 11 pairs per trial. The duration of trials ranged from 12 to 27 days. The number of resident mice in double enclosures was 2.3 times higher than the number in single enclosures ( $P < 0.001$ ,  $t$ -test), due primarily to an increase in females; they increased from 1.1 to 3.1 individuals per trial.

### Emigration

All emigrations (in double and single enclosure trials) occurred at night when mice were most active ( $n = 110$ ). Most emigrants (74%) left within 12 hours after the introduction of a pair of mice. All others left within 36 hours following introduction of a pair.

### Behavioral Observations

After introduction, mice moved around the perimeter of the enclosure in their initial fright response and exhibited behavior similar to that described by Crowcroft and Rowe (1963). Introduced mice hid under one of the first cover units they reached. If the unit was occupied or defended by a resident mouse, agonistic behavior (e.g., chasing, biting, and fighting) followed. Resident mice defended more than 1 cover unit, and newly added mice were chased from all defended units. If all cover units in an enclosure were defended, newly added mice often inspected the exit, but rarely crossed the water immediately and continued to explore the enclosures. I found 2 dead male mice at the end of the first double enclosure trial, and 1 dead male at the end of the second single enclosure trial. All dead mice showed evidence of bites that presumably resulted from fighting.

**Table 1.** Number of house mice classified as residents for trials in double enclosures with exits for emigration.

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<u>Trial#</u>	<u>Male Residents</u>	<u>Female Residents</u>	<u>Total No. of Residents</u>	<u>Pairs added</u>
1	2.0	3.0	5.0	7.0
2	3.0	4.0	7.0	8.0
3	2.0	4.0	6.0	11.0
4	3.0	4.0	7.0	7.0
5	1.0	2.0	3.0	5.0
6	1.0	3.0	4.0	7.0
7	1.0	4.0	5.0	6.0
8	1.0	1.0	2.0	6.0
<u><math>\bar{x}</math></u>	<u>1.8</u>	<u>3.1</u>	<u>4.8</u>	<u>7.1</u>

---

## DISCUSSION

The role of emigration in population regulation has not been clearly demonstrated in past studies due to difficulties associated with maintaining sufficient control over the test environment and with unambiguously identifying and enumerating resident and emigrant animals (Gaines and McClenaghan 1980). The outdoor enclosures I used subjected the test animals to "natural" weather conditions, but food and water were abundant and shelter was held constant throughout all trials. The enclosures excluded predators and immigration of animals, and mice that used the exits could clearly be defined as emigrants and not residents leaving during routine exploration (Nelson 1992). Mice residing in the enclosures could leave at any time through an exit, so their residency signifies that the test environment served as acceptable habitat for house mice (Nelson 1992).

Generally, mice introduced first stayed in an enclosure to the end of every trial. Mice added later, especially males, were more likely to be emigrants. Apparently, the test conditions encountered by the mice added first were adequate to trigger a settling or colonization response. Although resource levels were held constant, most mice added later were unable to colonize, presumably because of agonistic responses of resident mice. Prior residency generally conferred a behavioral advantage, even if individuals added later were larger than mice already residing in enclosures.

Emigrations occurred relatively quickly after new individuals were added to enclosures; 74% of emigrants left enclosures within 12 hours of an introduction of new mice. The social interactions that led to emigration must have happened quickly and been relatively intense.

I interpreted the emigration of a pair of mice soon after introduction of a pair, 3 times in succession (i.e., no net increase in the number of residents), as evidence that "full residency" or the short-term carrying capacity of an enclosure had been achieved. The carrying capacity of double enclosures was a little more than twice the capacity of single enclosures. Available cover units were never fully occupied due to the defense of these units by resident mice, even though food and water were provided in excess, supporting the conclusions of Brown (1953), Southwick (1955), and Crowcroft and Rowe (1963) that resident mice can successfully exclude immigrants and control access to resources below full utilization.

I cannot explain why the double enclosures held significantly more than 2 times the number of females than the single enclosures (3.1 and 1.1, respectively [ $P < 0.05$ , t-test]). Perhaps the added complexity of the tunnel joining the single enclosures enhanced partitioning of the enclosures among females and the tunnel may have provided the necessary cues and added area to accommodate more females.

The basic responses of mice to the environmental and social conditions in my enclosures were consistent with ecologically appropriate responses to similar conditions in nature (Matter et al. 1989). Mice in my enclosures could freely stay or emigrate at any time,

just as in nature. Mice encountering unoccupied and undefended cover units became residents and apparently excluded most mice added later from access to resources and triggered these "excess" individuals to emigrate. The defense of resources by residents and the emigration of excess individuals determined the number of animals able to reside in the enclosures. If the habitat use, spacing, and emigratory behaviors I observed in enclosures are representative of responses of animals in nature, animals that are established residents in an area should be able to control access to resources, just as the mice in my enclosures did. Because an area of habitat can be divided into a limited number of territories, spacing behavior by individual mice may limit the number of animals that can reside in a given area in nature.

Some biologists have argued that extrinsic forces are necessary to regulate animal numbers, including weather (Andrewartha and Birch 1954), predators (Errington 1936, Buehler and Kieth 1982), and diseases or parasites (May 1983). These forces either did not or were not allowed to act in my tests, and yet the number of resident animals was relatively constant. Thus, spacing behavior and emigration alone were sufficient to achieve consistent numbers of house mice in an open system. This is not to say that extrinsic forces of mortality (e.g., weather, predation, and disease) are unimportant to the abundance and distribution of animals. For example, predators may restrict prey to sites with dense cover and remove most individuals unable to find and hold such sites. But extrinsic forces are likely to act more heavily on emigrants forced into areas with inappropriate conditions than on

resident animals in high quality habitat. Thus, for species that show spacing behavior, extrinsic forces may be the proximate cause of death for many individuals, but their vulnerability to these forces may be largely the result of being emigrants.

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