HOMING TENDENCIES OF LARGE MAMMALS:
A REVIEW

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Abstract: Large herbivores (white-tailed deer [Odocoileus virginianus], mule deer [O. hemionus], and moose [Alces alces]) that were translocated >30 km usually settled <30 km from the release sites, but large omnivores (black bears [Ursus americanus], brown bears [U. arctos], polar bears [U. maritimus]) or carnivores (gray wolves [Canis lupus], and red foxes [Vulpes vulpes]) that were similarly translocated tended to move farther. The few individual herbivores and the many omnivores and carnivores that moved >30 km tended to move homeward. Of the taxa studied, the bears were the species most likely to return home from long distances (64-430 km), but the longest homing movement was by a white-tailed deer that returned 560 km to the Aransas National Wildlife Refuge in Texas. The possible role of olfaction in homing movements is discussed. Reintroduction efforts involving species that range widely before settling may require relatively large numbers of individuals to assure reproductive success.

Key Words: Homing mechanisms, reintroductions, translocations, orientation, navigation.

One factor in the success of reintroductions is the willingness of animals to remain where released. The desire to return home results in considerable movement by some species. Homing tendencies of mammals have been studied for more than 50 years, but basic questions remain as to whether animals that return home do so primarily by random movements, familiarity with large areas, or some means of navigation. Answers to this question may enable managers to better understand and predict movements of reintroduced mammals. Homing by small mammals was reviewed by Joslin (1977). The purpose of this paper is to review information on movements

of translocated large mammals as a beginning toward understanding their behavior and the mechanisms of mammalian homing.

Three levels of navigation ability were defined by Griffin (1955). Type I is simple orientation by means of familiar landmarks (visual or otherwise). Type II is the ability to move in a particular compass direction without reference to landmarks, and Type III, often called true navigation, is the ability of an animal in an unfamiliar area to orient toward home or some other goal beyond the range of sensory contact. The latter is the type of navigation ability needed for efficient homing from unfamiliar release sites. Homing pigeons (Walcott, 1974), swallows (Southern, 1959, 1968), and certain oceanic seabirds (Mazzeo, 1953; Kenyon and Rice, 1958) are thought to possess this ability (Emlen, 1975). Homing pigeons have homed from up to 1,600 km or more (Walcott, 1974), and seabirds have homed from up to 6,000 km at speeds of up to 510 km/day (Mazzeo, 1953; Kenyon and Rice, 1958).

Most studies of mammalian homing have involved capture-recapture studies of small mammals (Joslin, 1977) (Table 1). However, because capture-recapture studies generally provide little information on the exact path of individuals that return home or on the movements and fates of those that do not, those studies have not established whether or not mammals possess true navigational ability (Bovet, 1978). There is little direct evidence for the perceptual mechanisms and only scant evidence for the cues that may be used in homing (Joslin, 1977). Maximum distances that the various species of small mammals have homed vary with home range size (Bovet, 1978), but whether this is due to differences in familiar area or to differences in inclination to travel is unknown. Maximum distances also depend on experimental design. Translocation experiments with some small mammals involved only a few hundred meters, so recorded homing distances for those species are quite short, and questions remain as to whether they were truly translocated beyond the range of familiar sounds and odors (Joslin, 1977). Although a few individuals have returned from surprising distances, a high percentage of small mammals appear disinclined to travel long distances in unfamiliar range, and many have established home ranges near release sites (Murie and Murie, 1931; Robinson and Falls, 1965; Bovet, 1978).

Homing by Large Mammals

Deer

The tendency to remain near release sites was found in translocated white-tailed deer but a few individuals demonstrated unusual homing ability. In Texas, most (number not stated) of 8,727 deer that were translocated 100-600 km remained within 30 km of their release sites, according to kill records (Hahn, 1945; Glazener, 1948). However, 35 movements >30 km were recorded, and 17 of those were within 22.5° of home directions, which is significantly more than the 2.2 deer that would be expected to move that direction by chance ($\underline{X}^2$ = 99, 1 df, P <0.0001). Seven of the 17 that moved homeward reached home, traveling minimum distances of 130, 130, 240, 325, 530, 530, and 560km (Hahn, 1945; Glazener, 1948). These movements include the longest homing movements recorded for translocated North American mammals (Table 2). Similarly, in Oklahoma and Missouri, large but unstated numbers of deer were translocated. Again, most of them remained near their release sites, but 2 returned home from 72 and 120km away (Robb, 1953; Anon., 1958). In the northern states, white-tailed deer were translocated shorter distances. Again, the majority remained near their release sites, usually within 30 km (Bartlett, 1933; McBeath, 1941; Powell, 1952; Pietsch, 1954; Hamilton, 1962). The few that returned showed a pattern of decreased homing with increased translocation distance, as is commonly reported for small mammals. In Illinois, of 28 deer that were translocated 10-58 km, 19 were eventually killed an average of 3.2 km from their release sites, and 2 returned home distances of 10 and 40 km (Hawkins and Montgomery, 1969). In Michigan, 47 (24%) of 192 deer returned home from 35km away (Switzenberg, 1958, cited by Verme, 1973). In Indiana, 12 (25%) of 48 deer that were translocated 11-124 km moved toward home, with 7 (15%) reaching home (Hamilton, 1962). In Wisconsin, 1 of 6 returned home from 10 km away, 1 of 8 returned from 21 km away, and none of 18 returned from 160 km away (Dahlberg and Guettinger, 1956). Mule deer in New Mexico were similar; 5 of 8 returned home from 12 km away, 2 of 4 returned from 23-50 km away, and neither of 2 returned from farther away (Eberhardt and Pickens, 1979). The longest mule deer return (50 km) was by an adult buck that crossed the Rio Grande from the Sangre de Cristo Mountains

to his original capture area in the Jamez Mountains near Los Alamos (Eberhardt and Pickens, 1979).

Moose

   Moose that were translocated 700 km from Algonquin Provincial Park, Ontario, to the Upper Peninsula of Michigan showed movement patterns roughly similar to those of translocated white-tailed deer. Twenty-two (76%) of 29 moose (10 bulls, 19 cows) settled within 20 km of the release site. Of the 7 that moved farther, 2 bulls moved 35 and 290 km toward Algonquin Provincial Park, and the 5 others (1 bull, 4 cows) moved up to 71 km in nonhomeward directions (R.W. Aho, pers. commun.).

Black Bears

   Black bears differ from deer and moose in that very few individuals, mainly cubs and yearlings, remain near their release sites (Harger, 1970; McCollum, 1974; Alt et al., 1977; McLaughlin et al., 1981; J.R. Gunson, unpubl. data; Rogers, 1986). The majority leave within a week, with distances moved varying with translocation distance (Harger, 1970; Rogers, 1974). In the longest translocations, from Minnesota to Arkansas (>1,400 km), bears moved up to 418 km after release (Roger, 1974). No movements that far have been recorded for nontranslocated black bears. The tendency of black bears to move rather than settle after release has made this species the subject of numerous studies of homing ability, and the black bear has provided some of the most enlightening information on mammalian orientation. In 8 studies in 7 areas, 77 adults were translocated >64 km and recovered. Translocations of this distance would nearly always be into unfamiliar range according to movements of nontranslocated bears in 17 studies throughout the black bear range (reviewed by Rogers, 1987). After release and a period of wandering, 52 (68%) of the 77 moved within 22.5° of the homeward direction (Table 3). This is significantly more ($\underline{X}^2 = 48$, 1 df, $\underline{P} <0.0001$) than the 4.8 bears that would be expected to move that direction by chance. Further, the percentage moving homeward did not decline with increasing translocation distance between 64 and 271 km, which indicates that the homeward movements did not depend upon familiarity with the release area because fewer bears should be familiar with the more distant areas. Thirty-four

(44%) of the 77 reached home (Table 3). Of the 43 that did not, 18 (42%) moved in the homeward direction before they settled or were recovered. This again is significantly ($\underline{X}^2 = 9.3$, 1 df, $\underline{P} < 0.01$) more than would be expected by chance even though the 43 would include the individuals with poorest homing ability and any bears disinclined to return because they were not residents of the capture area. The fact that the 43 were significantly oriented toward home is evidence that homing was not accomplished by random movements or expanding search patterns. The fact that the studies were conducted in 7 different areas minimizes any effects of local physiographic features that might promote or inhibit homing. The means by which bears oriented and navigated homeward were effective to at least 271 km but apparently failed by 1,400 km because bears translocated from Minnesota to Arkansas (>1,400 km) moved in random directions after release (Rogers, 1974). Cub and yearling black bears showed poor homing success from all distances (Harger, 1970; Alt et al., 1977; Massopust and Anderson, 1984).

Brown and Grizzly Bears

Brown and grizzly bears have been studied less than black bears but appear to have homing abilities that are at least as well developed. Twelve of 23 adults returned from up to 258 km away after being translocated 145-286 km in southern Alaska (Miller and Ballard, 1982). All left the release areas. In Montana, each of 6 that were at least 2 years old returned from 26-48 km away, but only 3 of 13 returned from 54-262 km away, and none of 3 cubs and 2 yearlings returned from 19-54 km away (Thier and Sizemore, 1981). In Glazier and Banff national parks, each of 6 returned from 14-130 km away (Mundy and Flook, 1973). An adult female in southeastern Yukon returned home twice from 32 and 85 km away (Pearson, 1975).

Polar Bears

Polar bears may also have well-developed homing and navigational abilities (Beeman and Pelton, 1976). Polar bears that live on drifting, changing ice presumably navigate by other than familiar landmarks to return to previously visited areas (J.W. Lentfer, pers. commun. to Beeman and Pelton, 1976). However, their homing ability has not been adequately

tested because the only translocations of polar bears were to a commonly used migration route that may have been within familiar range (Stirling et al., 1977). In that instance, 40 polar bears were captured near Churchill, Manitoba, and released 300 km southeast on the shore of Hudson Bay (Stirling et al., 1977). The shortest land route was 480 km along the shore. At least 13 returned, including 3 males and a mother with cubs that returned in 14-24 days. Assuming that the land route was used, as was usual at that time of year because the bay was not frozen, the bears moved 20-34 km/day.

Gray Wolves

Five gray wolves that were pen-reared at Barrow, Alaska, were translocated 282 km (Henshaw and Stephenson, 1974). One returned to the home pen, and 3 were killed after moving 3, 140, and 160 km toward home. The 5th moved 160 km to an airport in a nonhomeward direction and was killed. The home pen was also near an airport, so the researchers suspected that all the movements were toward the sounds of large aircraft, which can be heard great distances on calm, cold days in that region (Henshaw and Stephenson, 1974). Whether the wolves showed true navigation or not, they demonstrated strong tendencies to leave the release site and return home. Wolves in Minnesota showed the same tendencies but were unable to return from such distances. Nine of 15 adults that were translocated 50-64 km returned home, but none of 20 that were moved 65-317 km returned home, and no pups returned from either distance (Fritts et al., 1984). Eleven radiocollared adults provided details of movements. All left the release area within 24 days and traveled alone. Their initial movements averaged only 33° off home directions, but the wolves veered off further when they encountered large open-pit mines or areas of human activity. Two of the wolves that returned home traveled in a variety of directions for 4 months before heading home. In Michigan, 3 pack members that had been translocated 450 km from Minnesota remained together after release. They moved 60 km west southwest, again only 33° off the home direction, explored an area of 4,224 km for 6 weeks, and settled 93 km southwest of the release site (Weise et al., 1975). A 4th wolf that was similarly translocated initially moved 52km

south southeast and showed no consistent homeward movement (Weise et al., 1975). On Isle Royale, tame wolves that escaped from pens were subsequently captured and translocated 48 km (Mech, 1966). All returned the next day, but how much of the island they had become familiar with before being translocated is unknown.

Other Species

Homing by other species of large mammals has not been studied specifically although a few cases of homing have been reported. A translocated coyote (Canis latrans) returned home 48 km in Arizona (Danner and Fisher, 1977). An adult female kit fox (V. macrotis) returned home 32 km in Utah (Egoscue, 1956). A house cat in England returned 217 km from its new home to its old one (Carthy, 1956). An adult female red fox returned home 56km in 12 days in Iowa (Phillips and Mech, 1970), but none of 21 red foxes that Marcstrom (1968) moved 20-170 km in Sweden returned despite travel of up to 125 km. Only 1 of 9 adult female red foxes and none of 171 pups returned after being translocated 3-173 km in Iowa (Andrews et al., 1973). The adult that returned was translocated 14 km (Andrews et al., 1973).

Discussion

Translocated large omnivores or carnivores generally have shown greater movement after release than have herbivores. Where omnivores or carnivores are being translocated for reintroduction, the long movements after release may result in lower densities around release areas than would be likely with herbivores, which could reduce chances of mating and establishment of breeding populations. Reintroduction efforts with omnivores or carnivores may require larger numbers to compensate for their greater movement. Even among some herbivores, movements may be great enough to reduce reproductive success. Only 7 of 14 moose cows reproduced in Michigan in 1986 with poorest reproduction occurring in cows that moved farthest from the release site to areas of lowest moose density (Schmitt and Aho, 1987).

The fact that a high percentage of herbivores settle near release sites in unfamiliar range would at 1st seem to indicate that they have poor homing ability. However, where large numbers have been translocated,

a few individuals have returned home from remarkable distances. Most notable are the return by a white-tailed deer from 560 km away (Hahn, 1945) and a return by a deer mouse (Peromyscus maniculatus) from 3.2 km away (Murie and Murie, 1931) which indicate that at least a few individuals of these species have the inclination and ability to return home.

The senses involved in mammalian navigation have been little studied. Homing pigeons have been intensively studied, and previously unknown sensory abilities were found. They can detect polarized light, untraviolet light, very low frequency infrasounds, and changes in atmospheric pressure (Delius et al., 1976; Delius and Emmerton, 1978; Kreithen, 1978), but the extent to which these senses are used in homing has not been established. Homing pigeons may also detect the earth's magnetic field because magnetite has been found in their heads (Walcott et al., 1979). However, even if they have geomagnetic compass sense, the mechanisms of orientation in unfamiliar areas remain a mystery because a mental map is still needed to use this sense. Recent studies have shown that homing pigeons have a good sense of smell and that odors may be important in the formation of the mental map (Walraff, 1983). Papi et al. (1973) proposed that young pigeons learn the odors of the loft area as well as wind-borne foreign odors. Pigeons raised in cages with wind deflectors that deceived the pigeons about wind direction made predictable errors in orientation when released in unfamiliar areas >60 km from home (Baldacinni et al., 1975; 1978; Fiaschi et al., 1981). Pigeons released >60 km from home showed poor homing success unless they had access to olfactory cues during translocation (Ioale et al., 1983).

The possibility of sensory contact with the home environs has not been excluded in even the longest homing instances by mammals and requires additional study. The wolves that homed from 282 km away may have heard air traffic from the airport adjacent to their home pen in Alaska (Henshaw and Stephenson, 1974), and the deer that returned up to 560 km from north central Texas to the Aransas National Wildlife Refuge on the shore of the Gulf of Mexico (Hahn, 1945; Glazener, 1948) may have smelled the ocean when breezes were from the south southeast. Black bears (J.R. Gunson, unpubl. data; Rogers, 1986) and wolves (Fritts et al., 1984) made long movements in several directions in some cases before moving quickly

and directly homeward. The possibility has not been excluded that these movements enabled detection of scent gradients that aided orientation. Bears translocated >1,400 km showed no homeward orientation (Rogers, 1974). If homing by mammals depends upon sensory contact with the home area, their homing would not conform to Griffin's (1955) definition of true navigation. Although the mechanisms of mammalian homing have not been determined, data obtained for the more intensively studied species indicate that random movement or expanding search patterns are not the primary mechanisms (Robinson and Falls, 1965; Rogers, 1986, 1987) and that familiarity with release areas is not a prerequisite for homeward orientation. More detailed information on movements and sensory abilities of mammals is needed to obtain positive information on the perceptual mechanisms and cues used. Adult black bears may be suitable subjects for detailed studies of movements because adults are strongly inclined to return home and are large enough for telemetry and observation studies.

Acknowledgement

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Table 1. Longest homing movements recorded for translocated North American small mammals.

Species	Distance/km	Source
Indiana myotis (Myotis sodalist)	320.0	Barbour et al. (1966)
Little brown myotis (M. lucifugus)	193.0	Leffler et al. (1979)
Eastern cottontail (Sylvilagus floridanus)	4.8	Bowers. (1954)
Gray squirrel (Sciurus calolinensis)	4.5	Hungerford and Wilder (1941)
Deer mouse (Peromyscus maniculatus)	3.2	Murie and Murie (1931)
Southern flying squirrel (Glaucomys volans volans)	1.6	McCabe (1947)
Yellow-pine chipmunk (Eutamias amoenus)	1.6	Broadbooks (1970)
Cotton rat (Sigmodon hispidus)	1.5	DeBusk and Kennerly (1975)
St. Kilda field mouse (Apodemus sylvaticus hirtensis)	0.853	Boyd (1963)
Red squirrel (Tamiasciurus hudsonicus)	0.7	Layne (1954)
Eastern chipmunk (Tamias striatus lysteri)	0.64	Layne (1957)
Cotton mouse (Peromyscus gossypinus)	0.64	Griffo (1961)
Townsend's mole (Scapanus townsendii)	0.45	Giger (1973)
Meadow vole (Microtus pennsylvanicus)	0.42	Robinson and Falls (1965)
Great Basin pocket mouse (Perognathus parvus)	0.4	Broadbooks (1961)
Western harvest mouse (Reithrodontomys megalotis)	0.3	Fisler (1966)
White-footed mouse (Peromyscus leucopus)	0.21	Stickel (1949)

Table 1. Longest homing movements recorded for translocated North American small mammals. Cont.

Species	Distance/km	Source
Oldfield mouse (*Peromyscus polionotus*)	0.194	Gentry (1964)
California vole (*Microtus californicus*)	0.18	Fisler (1962)
Brush rabbit (*Sylvilagus bachmani ubericolor*)	0.15	Chapman (1971)

Table 2. Longest homing movements recorded for translocated North American large mammals.

Species	Distance/km	Source
White-tailed deer	560	Hahn (1945)
Polar bear	480	Stirling et al. (1977)
Gray wolf	282	Henshaw and Stephenson (197?)
Grizzly bear	258	Miller and Ballard (1982)
Black bear	229	Harger (1970)
House cat	217	Carthy (1956)
Red fox	56	Phillips and Mech (1970)
Mule deer	50	Eberhardt and Pickens (1979)
Coyote	48	Danner and Fisher (1977)
Kit fox	32	Egoscue (1956)

Table 3. Movements of translocated black bears at least 2 years old.[a]

Translocation distance/km	Bears translocated and recovered (N)	Bears moving within 22.5 of home directions (%)	Bears that reached home (%)
64-120	54	65	50
120-220	18	72	33
220-271	5	80	20

[a] Data compiled from the following reports from 7 states and provinces: Erickson et al. (1964), Harger (1970), McCollum (1974), Payne (1975), Orff (1982), Massopust and Anderson (1984), Rogers (1986), J.R. Gunson (unpubl. data).