active hunters (*15*), nearsighted loxoscelids and scytodids wait until prey becomes entangled in their crude snares before they use venom or a zigzag squirt of oral glue to subdue it. It is commonly known that the brown recluse can survive indoors for months or even years without food and water. Perhaps members of these families, more so than other spiders (*10*), can rapidly raise and depress their general metabolism to adjust to a particular situation (*16*).

Although there was no significant difference ($P > .05$) in body weights of large (230 to 630 mg) web weavers and hunters, the former group had significantly greater ($P < .001$; Student's t-test) heart rates (Fig. 2). Both types of female spiders use silk on some occasions during their lives (for example, to encase their eggs), but the degree to which they rely on it is different (*15*). Large hunters, typified by wolf spiders, ambush almost any small animal moving near them and attempt to overcome it by force. In contrast, web-building species are characterized by a sedentary existence, becoming so committed to a life on webbing that their delicate limbs and pendulous abdomens make locomotion awkward on a smooth, horizontal surface. We suggest that the superficially apparent sedentary nature of web-weaving spiders is deceptive. If the energy expended for silk production and utilization were added to predation energy budgets, it might show that orb weavers expend as much or more energy as active predators like lycosids. Hence, the ecological efficiency of web species could be much lower than predicted (*17*).

JAMES E. CARREL
R. D. HEATHCOTE*
Dalton Research Center and *Division of Biological Sciences, University of Missouri–Columbia, Columbia 65201*

References and Notes

1. S. F. Johnson and J. A. Gessaman, *Utah State Univ. Monogr.* **20**, 44 (1973).
2. D. A. Parry and R. H. J. Brown, *J. Exp. Biol.* **36**, 423 (1959); *ibid.*, p. 654.
3. C. H. Ellis, *Biol. Bull.* **86**, 41 (1944).
4. D. M. Stewart and A. W. Martin, *J. Comp. Physiol.* **88**, 141 (1974).
5. R. S. Wilson, *J. Insect Physiol.* **13**, 1309 (1967).
6. R. G. Sherman and R. A. Pax, *Comp. Biochem. Physiol.* **26**, 529 (1968).
7. C. R. Bursey and R. G. Sherman, *Comp. Gen. Pharmacol.* **1**, 160 (1970).
8. Spiders were individually enclosed in clear plastic culture dishes with small holes for ventilation, or in cardboard boxes modified for web building [P. N. Witt, *BioScience* **21**, 23 (1971)]. Both containers could be oriented either horizontally or vertically, whichever position is characteristic of the species. This arrangement permitted spiders to assume a typical resting posture. After addition of distilled water to prevent desiccation, the dish or box was clamped to a micromanipulator and positioned over a He-Ne continuous wave laser (Metrologic Instrument) with a wavelength of 632.7 nm and a power output of about 1 mw.
9. Monochromatic red light emitted by a low-intensity He-Ne laser probably causes little neural excitation and virtually no heating or tissue damage in spiders. Spiders did not move when the laser beam was pointed at their eyes or other body parts. Furthermore, after a spider had rested for 1 hour or longer, neither continuous nor intermittent transillumination evoked a noticeable change in its heart rate. The elevation of body temperature in an anesthetized *Lycosa ceratiola* (1 g) after 1 hour of continuous illumination was 0.1°C above background temperature, as detected by a thermocouple inserted in the abdomen beside the heart.
10. J. F. Anderson, *Comp. Biochem. Physiol.* **33**, 51 (1970); *Ecology* **55**, 576 (1974).
11. Spiders were kept individually at room temperature (23° to 26°C) under constant fluorescent illumination (about 200 lux) either in clear plastic containers partially filled with moist sand or in special boxes (*8*). Water was supplied daily for drinking and humidification. Spiders were fed live mealworms (*Tenebrio molitor*) or cockroaches (*Nauphoeta cinerea*) weekly in numbers sufficient to keep their body weights relatively constant. Animals were acclimated for 3 to 4 weeks to these conditions. All measurements were made 2 to 6 days after a meal, usually between 1000 and 1400 hours CDST., although readings taken at other times of the day in two individuals of five species (*Aphonopelma chalcodes, Loxosceles reclusa, Lycosa ceratiola, Argiope aurantia,* and *Misumenoides formosipes*) were not significantly different ($P > .1$; Student's t-test). The heart rate of each spider was determined on three or more separate occasions spanning several weeks.
12. W. S. Bristowe and J. Millot, *Proc. Zool. Soc. (London)* **103**, 1015 (1933); I. Mikulska and W. Kokocinski, *Bull. Acad. Pol. Sci. Cl. 2 Sér. Sci. Biol.* **13**, 533 (1965).
13. C. L. Prosser, *Comparative Animal Physiology* (Saunders, Philadelphia, 1973), p. 837.
14. With the use of the data of Anderson (*10*) for adult female spiders, the relation between standard metabolic rate (M) (microliters of O_2 per gram per hour) and body weight (W) (milligrams) is $M = 947\,W^{0.408}$ ($r = .91$; $P < .001$). This exponential is equal to the one in the heart rate (H)–body weight (W) regression of Fig. 2. It follows the $M/H = 2.25$. However, because these respiration rates were obtained at 4°C less than our heart rates, we estimate the isothermal ratio to be about 2.5.
15. W. J. Gertsch, *American Spiders* (Van Nostrand, New York, 1949).
16. If spiders are in a depressed metabolic state, an arousal period should be necessary for them to respond to a disturbance. We frequently have observed in the laboratory and at home that quiescent brown recluse spiders do not respond immediately when prodded, whereas their recently active cohorts do. Similar observations have been made with some wolf spiders of the genus *Lycosa*.
17. F. Enders, *Am. Nat.* **109**, 737 (1975), and references therein.
18. We thank R. Bunn, C. Higgenbotham, and S. Hata for technical assistance, and W. R. Enns, W. J. Gertsch, and H. K. Wallace for identification of spiders; the director and staff of the Archbold Biological Station, Lake Placid, Florida, for assistance and hospitality; and S. B. Chaplin for reading the manuscript. Supported in part by the Bache Fund of the National Academy of Sciences.
* Present address: Biological Laboratories, Harvard University, Cambridge, Mass. 02138.

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Intraclonal Histocompatibility in a Parthenogenetic Lizard: Evidence of Genetic Homogeneity

Abstract. *A total of 175 skin grafts were transplanted among 20 individuals belonging to two separate populations of the parthenogenetic lizard* Cnemidophorus uniparens. *Of these, 98.8 percent were permanently accepted, which indicates that all individuals of each population may be genetically identical. These results further suggest that large populations or the entire species may consist of one clone derived from a single individual.*

It is generally assumed with regard to parthenogenetic species that individuals within a clone are genetically identical, although the extent of genetic uniformity has not been clearly ascertained experimentally. Support for this assumption has been obtained by various tissue-grafting studies showing that allografts exchanged among conspecific individuals are not rejected (*1–4*). The majority of these studies, however, have involved a limited number of individuals from any one single population. For instance, in the case of the unisexual fish *Poecilia formosa*, some of the transplantation experiments involved the descendants of one or two individuals (*2*). In other studies in which allografts were exchanged among substantial numbers within a population (*3, 4*), the grafts were exchanged only between pairs, so that each individual received and donated one graft. Only Maslin (*3*) has intergrafted among several individuals to test for potential histoincompatible clones within a single natural parthenogenetic population. Using an elaborate transplantation scheme, he intergrafted among six parthenogenetic lizards, each donating to and receiving grafts from the other five. A total of 30 grafts were transplanted and all were permanently retained.

These data do not, of course, rule out the possibility that occasional histoincompatible individuals may exist within single clones, but their detection is made difficult by inherent limitations in the existing surgical techniques employed to excise the grafts. For instance, in the case of *P. formosa*, whole organs, such as fins or hearts, are transplanted, which often requires killing the donors. In the case of parthenogenetic lizards, the use of skin grafts is more practical since donors need not be killed, and several grafts can be transplanted on one individual. Nevertheless, present techniques require conventional surgery, which is not only tedious but also imposes a limit on the size of the graft and therefore on the total number that may be transplanted to one individual. If genetic differences exist within clones, their detection will be maximized in pro-

portion to the number of intraclonal individuals tested. Conversely, the absence of any histogenetic differences among a large sample provides a greater measure of the degree of similarity within a clone. This study was conducted to determine in greater detail the degree of histogenetic homogeneity within clones of the triploid parthenogenetic lizard *Cnemidophorus uniparens*. A new mechanical technique used for excising the grafts (i) provides an enormous reduction in excision time, (ii) allows cutting grafts of uniform size and shape, and (iii) permits the excision of smaller grafts than can be cut by conventional methods, thus allowing a larger number to be transplanted per individual.

Specimens of *C. uniparens* used for this study were collected from two localities in New Mexico: Bosque del Apache National Wildlife Refuge (Socorro County) and along the Rio Grande in the vicinity of Frau Cristobal Mountain, around 26 miles north of Truth or Consequences (Sierra County). Ten specimens from each locality were used. Those from Bosque del Apache were collected on 22 June 1972 and those from Cristobal Mountain on 6 to 19 June 1973. Individuals collected in a small geographic area (1 to 2 acres) are assumed to be members of one clone. Each specimen was permanently referenced by amputating specific digits. Animals were immobilized by placing them on a suspension of crushed ice. No interclonal grafts were attempted; therefore, each animal donated to and received grafts from only individuals assumed to be members of its clone. Before surgery, the skin on the dorsal side, where the grafts were to be excised, was coated with a layer of surgical adhesive (Aeroplast dressing, Parke-Davis) and allowed to dry. After each site was prepared, the skin was lifted with forceps so that the coated area was folded evenly. The folded skin was snipped approximately 1¼ mm deep with a Ztorz biopsy punch; this removed a double-layered skin crescent, which unfolded to a round piece approximately 2½ mm in diameter. Each allograft was placed perpendicular to the recipients' skin pattern in order to distinguish the grafts after healing (Fig. 2) (*5*). After blood on the edge of the graft was allowed to dry for a few minutes, the surrounding area was coated with adhesive to prevent the grafts from being prematurely discarded. A skin transplantation scheme similar to that of Maslin (*3*) was employed for exchanging the grafts. The dorsal skin surface was divided into longitudinal halves and each partitioned into five graft sites numbered 1 through 5 on the left side from head to tail and 6 through 10 on the right side. Each animal, irrespective of its permanent code, was then assigned a number from 1 to 10. No grafts were excised from the site corresponding to the number of the animal. For instance, site 1 was left intact on animal 1, site 2 on animal 2, and so forth. Also, each set

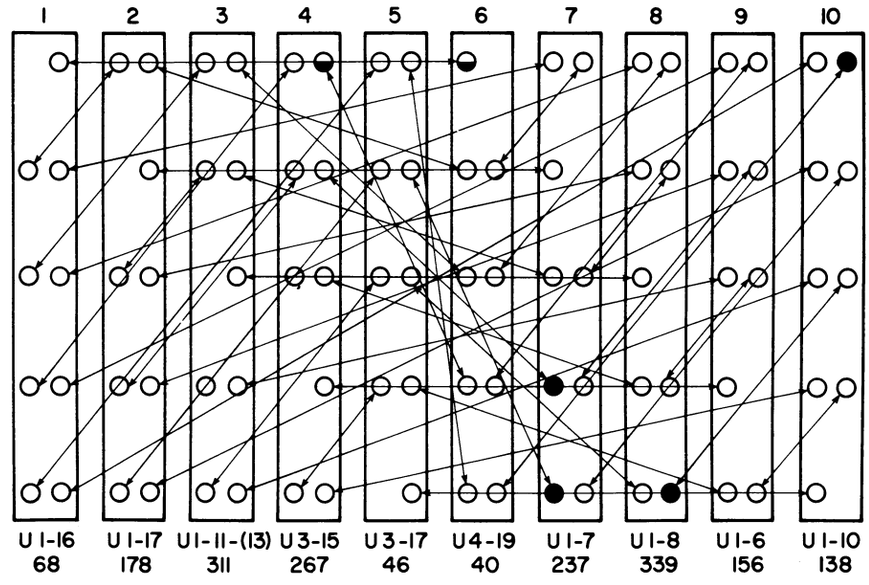

Fig. 1. Scheme showing allograft transplantation between ten intraclonal individuals of *C. uniparens*. Each bar represents an individual lizard. Circles within bars represent allografts and double arrows indicate a reciprocal transplantation exchange. Numbers immediately below the bars are lizard reference codes and numbers below the codes are animal survival times in days from transplantation date; open circles, no rejection; half-closed circles, slight graft loss; and closed circles, complete loss.

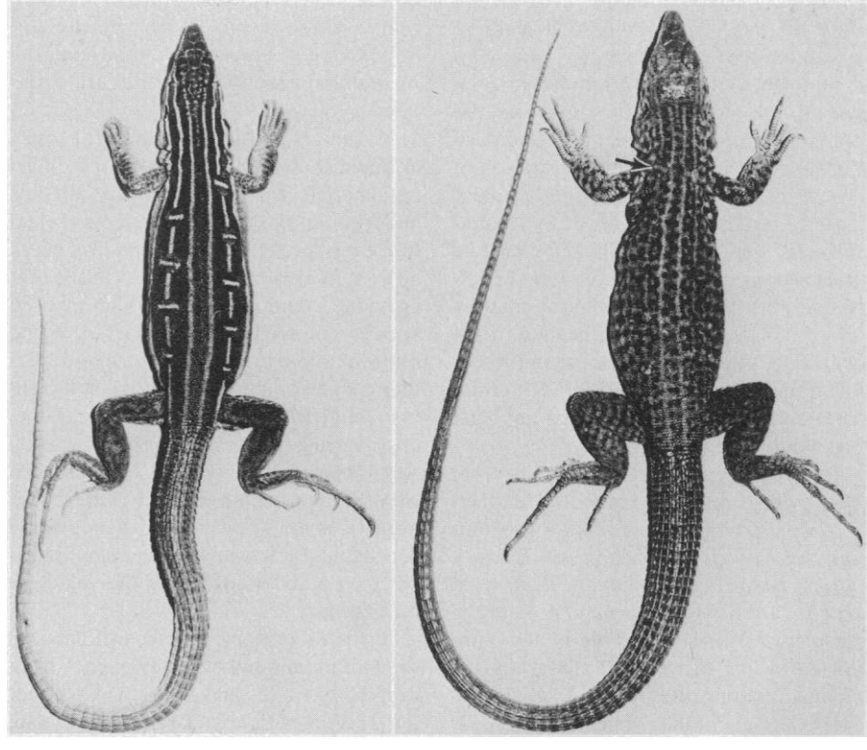

Fig. 2. (Left) Dorsal view of *C. uniparens*, a parthenogenetic lizard, showing nine permanently accepted allografts (indicated by transverse bars) received from nine different individuals of its clone. (Right) The same view of *C. tigris*, a bisexual species, showing barely discernible scarred sites of ten rejected allografts received from ten different conspecific individuals of its own population.

of reciprocal transplants was exchanged so that the graft site corresponded to the animal number (Fig. 1).

A total of 85 grafts rather than the expected 90 were exchanged among the ten individuals from Bosque del Apache. One individual (U8-18) died during surgery; only four of its nine potential grafts were donated. Except for the partial atrophy of one graft, there were no signs of rejection, and all 85 were permanently retained until either death or inadvertent loss of the recipient. Survival times for each specimen are as follows: U4-14, 42 days; U4-19, 50 days; U5-6, 279 days; U5-9, 160 days; U5-16, 142 days; U6-17, 145 days; U7-14, 93 days; U7-19, 120 days; U8-18, died after surgery; and U9-10, 140 days. Similar results were obtained with individuals from Cristobal Mountain. All 90 grafts were successfully transplanted in this case, but four became detached a few days after surgery and were eventually discarded. An additional two underwent partial atrophy, but otherwise healed normally and were permanently retained. Details of this experiment are listed in Fig. 1.

Of 175 grafts transplanted among 20 individuals, only four may have been rejected. However, there are two reasons to suspect that these rejections were caused by errors in technique rather than by actual histoincompatibility. (i) In each of these transplants an excessive amount of the surgical adhesive was accidentally introduced on the underlying tissue of the donor graft site while the grafts were being transplanted. Ordinarily, the adhesive dries on the surface of the graft without coming into contact with the exposed tissue of the evacuated recipient site. Occasionally, however, a graft is accidentally moved while the adhesive is still wet and the tissue may be injured or prevented from healing. (ii) If each rejection were due to actual histoincompatibility, rejection of all grafts from individuals that rejected at least one would be expected.

In any case, the fact that 99.8 percent of the grafts were permanently retained provides strong evidence that a substantial number of individuals of *C. uniparens* are genetically identical, at least with regard to histogenes and possibly to their entire genotype. This is also supported by the fact that all allografts exchanged among the bisexual species *C. tigris* are eventually rejected (Fig. 3). These results further indicate that each of these two clones and perhaps both, or even the entire species, may have been derived from one individual. However, this hypothesis can only be tested by showing histocompatibility between distantly spaced populations of this species. In another skin-grafting study (*5*), I showed that parthenogenetic species inhabiting uniform habitats, such as *C. neomexicanus* in the Rio Grande Valley, show genetic uniformity throughout extensive areas of their range, whereas species occupying diverse habitats, such as *C. velox* in the Four Corners region of southwestern United States, display genetic differences in different parts of their range. These results agree with the current thought in genetics that environmental and genetic uniformity are correlated.

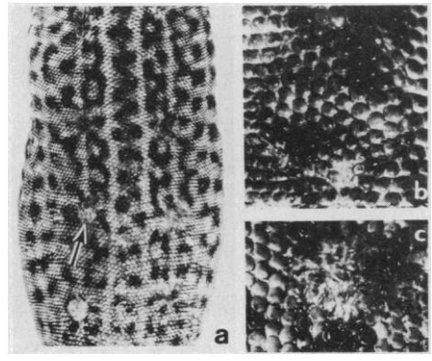

Fig. 3. Enlarged view of graft sites from *C. tigris*. (a) Dorsal torso showing eight rejected allografts. (b) Normal autograft indicated by arrow on left shoulder in Fig. 2. Graft is circular and covers around 80 scales. (c) Rejected allograft scar indicated by arrow in (a). Scar is around one-fourth the size of the original graft in (b).

Maslin (*3*) and Cuellar and McKinney (*6*) have shown that one extra and different genome (in tests between diploids and triploids) is capable of inducing rejection even though the donor and recipient share two identical genomes. On the other hand, I demonstrated (*5*) that even in species believed to be comprised of one uniform ploidy, as in the triploid parthenogenetic lizard *C. velox*, sufficient histocompatibility differences may accrue to cause rejection among distantly separated members of this species. Just exactly how extensive the differences must be is not known in parthenogenetic lizards, nor is it known how many different genes are involved in the rejection process.

In the laboratory mouse, estimates of the minimum number of histogenes have ranged up to 29, and the actual number may be considerably larger (*7*). Among the 13 histocompatibility loci known (*H-1* to *H-13*), rejection rates vary enormously depending on the immunologic strength of the particular locus (*8*). For instance, allelic differences at the *H-1* and *H-2* loci induce complete rejection of skin allografts in 8 to 20 days while differences at some of the weakest loci, such as *H-9*, *H-10*, and *H-12*, may require more than 300 days. In fact, in certain combinations complete rejection is never achieved. Rejection caused by differences at the strong loci results in complete graft destruction and ulcer craters at the graft site, whereas with the weak loci the graft is slowly replaced by the donors' scar tissue (*8*). In lizards complete rejection of xenografts occurs in about 12 days (*3*, *4*, *6*). It seems probable that in parthenogenetic lizards, too, an individual possessing an allelic difference in a strong locus would be histoincompatible with all other individuals in the same clone. Therefore all allografts, rather than a single one, should be rejected by the mutant recipient unless some of the donors shared identical loci. In that case the donors also should be histoincompatible with the normal members of the same clone.

Exactly how many genetically different individuals exist in natural parthenogenetic populations may be very difficult to determine, since testing even as few animals as reported here requires extensive time and effort. Nevertheless, this problem can be simplified by testing for differences between clones rather than among clones. Then, if two or more distantly spaced clones are found to be histocompatible, one may reasonably assume that all individuals between such clones may be identical. This is what I found in a study with the parthenogenetic lizard *C. neomexicanus* (*5*). Of 132 grafts interchanged among and between three populations spaced along 160 miles of their range, only a single graft underwent rejection, although the reciprocal allograft was permanently retained; this suggests that all individuals within this range are genetically identical, or nearly so. Even though this single graft was retained until the recipient's death 86 days after transplantation, it was reduced to approximately one-third its original size and its scales were abnormally crimped and pigmented. There is little doubt that rejection would eventually have been achieved but at a very slow rate, perhaps equivalent to the slow rates caused by differences at the weakly antigenic loci in mice. Signs of rejection caused by differences at such loci proceed slowly; therefore, some of the "normal" grafts in the present study might eventually have been rejected if their recipients had survived much beyond 50 to 100 days. Nevertheless, even when rejections proceed slowly in lizards, evidence

of rejection becomes apparent much earlier than 50 days (*3, 5, 6*).

One hypothesis to explain graft rejection among individuals of a parthenogenetic clone is that mutations might result in the loss of synthesis of specific antigens normally present on the cell membrane. If so, the difference would lie in the individual rejecting the allograft rather than the individual donating the rejected graft. For instance, assume that one individual possesses three antigens (A, B, and C) and another only two (A and C) because of a mutation in the *B* locus that prevented the formation of B proteins. Then the mutant individual would recognize the B antigen from the normal one and reject its graft, whereas the normal one would accept grafts from the mutant since they both shared identical antigens. If such mutants actually exist and could be effectively detected, one could determine with precision (made possible only by a system of parthenogenetic reproduction) the natural mutation rate for one set of genetic loci. Perhaps further refinement of the new technique described here may eventually lead to an accurate determination of these rates.

ORLANDO CUELLAR

Department of Biology,
University of Utah,
Salt Lake City 84112

References and Notes

1. W. V. Healy, P. S. Russel, H. K. Poole, M. W. Olsen, *Ann. N.Y. Acad. Sci.* **99**, 698 (1962); K. D. Kallman, *Evolution* **16**, 497 (19[illegible] R. M. Darnell, E. Lamb, P. Abramoff, *ibid.* **21**, 168 (1967).
2. K. D. Kallman, *J. Genet.* **58**, 7 (1962).
3. T. P. Maslin, *J. Exp. Zool.* **166**, 137 (1967).
4. O. Cuellar and A. G. Kluge, *J. Genet.* **61**, 14 (1972).
5. O. Cuellar, *Evolution*, in press.
6. ——— and C. O. McKinney, *J. Exp. Zool.*, in press.
7. D. W. Bailey and L. E. Mobraaten, *Genetics* **50**, 233 (1964); *Transplantation* **7**, 394 (1969).
8. R. J. Graff, W. Hildemann, C. D. Snell, *Transplantation* **4**, 425 (1966).
9. Supported in part by NIH biomedical science support grant RR07092 to the University of Utah and NIH grant 1 RO1 GM 19533-01 to O.C. I thank R. Montegomery and C. Smart for transplanting the grafts and selecting the biopsy punch, R. Ashburn and C. Smart for excellent photographic assistance, J. Hibbs and D. Steinmuller for helpful discussion, M. C. Rechsteiner and R. A. Schlegel for advice and critical review of the manuscript, and H. Cuellar and my family for assistance in collecting specimens.

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Migration Reversal: A Regular Phenomenon of Canada Geese

Abstract. *Migration from a nesting to a wintering ground and back again in autumn was detected each year during a 3-year study of individually identifiable Canada geese* (Branta canadensis). *Reverse migrants were primarily yearling, nonbreeding individuals and others of nonfamily status.*

Bird migration is normally considered as an orderly departure and return to the same area with the changing seasons. Flocks migrating opposite to the usual direction are uncommon, and causes are usually attributed to untoward weather conditions (*1*). My study of Canada geese (*Branta canadensis*) demonstrated regular occurrence of migration to wintering grounds and return to the nesting area in autumn among a small portion of the population. Reverse migrants were primarily 1-year-old, nonbreeding individuals and others not associated with families, which dominate goose society.

During July, August, and early September of 1968, 1969, and 1970, 1523 geese were captured and marked with individually identifiable plastic neck collars (*2*) and released at a marsh on the southeastern shore of Lake Manitoba (50°30′N, 98°W) 96 km northwest of Winnipeg, Manitoba, Canada. Age and sex of geese were determined by plumage and cloacal characters (*3*). Marked geese were observed at the marsh for an average of 2 days per week between 20 September and 20 November, during which all normal and reverse autumn migrations of this flock occurred. The main wintering site for this population was at Rochester, Minnesota (44°N, 92°20′W), 855 km southeast of the banding site (*4*). Marked geese observed in Rochester during autumn were recorded sporadically by me and by cooperators.

Canada geese mature sexually at 2 years of age (*3*). Three age classes were identified: immatures—banded and observed during the summer and autumn in which they hatched; yearlings—1½ years of age; adults—more than 2½ years of age. Most yearlings were away from the marsh at banding time at a distant molting site (*5*), but they returned to their natal marsh in autumn. Most observations (94.1 percent) of yearlings were made in 1969 and 1970 and represent surviving geese banded when immature the previous year.

Table 1. Number of marked Canada geese in relation to migration pattern.

Age	Migration	
	Normal	Reverse
Adult	477	10 (2.1 percent)
Yearling	223	13 (5.5 percent)
Immature	866	5 (0.6 percent)

Twenty-eight of 1594 marked geese (1.8 percent) identified in Manitoba during autumn 1968, 1969, and 1970 migrated to, and were seen at, Rochester, Minnesota, and then seen again in Manitoba in the same autumn. The length of stay of these geese at Rochester was imprecisely known because of irregular observation, but different individuals remained at least 2, 8, 10, 17, 42, and 61 days before returning to Manitoba. Irregular observation at Rochester also indicates that there could have been other reverse migrants that were undetected. Reverse migrants were predominantly yearlings ($\chi^2 = 26.56$; 2 d.f.; $P < .001$) (Table 1). There were no differences within any age class in the proportions of the sexes that participated in reverse migration.

Canada geese have a complex social organization. Goslings normally stay with parents for the first year of life and yearlings may rejoin parents, form pairs or sibling groups, or be unattached (*6*). Some families include goslings other than those hatched by the adult pair, and these associations are termed gang brood families (*7*). Marked geese observed in autumn in Manitoba were categorized as to their social relations based on stereotyped displays and unity in aggression, flying, and feeding, which indicate familial bonds (*6*)—as well as on repeated observation of associations of the identifiable birds of known age, sex, and history (Table 2).

Reverse migrant adults were primarily of unidentifiable social status and not birds with families ($\chi^2 = 21.64$; 5 d.f.; $P < .001$). Single adults and even pairs were unaggressive (*6*) and therefore difficult to identify as to social relations, especially if mates were unmarked, because of the low frequency of behaviors used to identify social positions. One adult male participated in reverse migration in both 1969 and 1970 and was a single in one year and of unidentified status in the other.

There was not a significant difference among social classes of yearlings that participated in reverse migration ($\chi^2 = 3.16$; 5 d.f.; $P > .5$). As with adults, single yearlings were difficult to identify. Even sibling groups were difficult to ascertain when all members were not marked and identified from observations as immatures. Yearlings that formed a pair bond were usually together and none par-