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 (1962); 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.

30 January 1976

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-

Table 2. Social status of marked Canada geese in relation to migration pattern.

Status	Migration					
	Adult		Yearling		Immature	
	Normal	Reverse	Normal	Reverse	Normal	Reverse
Family*	252	0	1	0	432	1
Gang brood family	11	2			135	0
Paired—no young	60	1	19	0		
Sibling group	5	0	27	3†		
Rejoin parents			34	2‡		
Single	17	1	19	2	23	1
Unknown	132	6	123	6	276	3
Total	477	10	223	13	866	5

*Includes pairs with 1-year-old (or older) young with or without immatures. †Three siblings always together migrated back as a group. ‡Variable behavior—sometimes with parents, sometimes as a single or with a sibling.

ticipated in reverse migration. Yearlings in sibling groups usually stayed together, and one of these groups participated in reverse migration. Yearlings rejoining their parents and new young were variable in behavior and not always in association with their families; these were probably singles when they participated in reverse migration because their parents were not observed with them.

Immatures in identified families did not reverse migrate in proportion to those unclassified as to status or those which were singles ($\chi^2 = 8.34$; 3 d.f.; $P < .02$). Immatures in families were frequently separated temporarily from their parents during feeding because of the large numbers of geese crowded into a small area where food was artificially provided. It was during these feeding periods that most observations of marked birds were made and, as a result, I was indecisive on the status of many young.

Single geese, particularly yearlings, are much more variable in daily roost and feeding locations and flight patterns than are families (*6*). They tend to join in flight with geese taking off near them, whereas adults with young maintain consistent patterns. Return to previously used areas is a major mechanism of reunification of family members. Yearlings are also less traditional in migration patterns than adults (*8*). The strong gregarious nature of geese, coupled with the following behavior of yearling and nonfamily geese, results in some interchange with other flocks and populations and probably accounts for the unusual but regular occurrence of these reverse migrations. Strong attachments to, and seeking of, family members (*6, 9*) probably motivated their return and to the natal marsh or autumn concentration locality.

Of the 28 reverse migrants, 21 returned again in the same autumn to Rochester, Minnesota. Of the other seven, the fate of two was unknown, one was shot in Manitoba and another in Iowa, one was observed in Missouri, and two were observed in Kansas. Irregular migration behavior by yearlings and singles could provide a major mechanism of gene flow, even though one of small proportions, between populations as localized and traditional as Canada geese, which exhibit marked isolationism and show geographic variation in morphology (*4, 10*).

DENNIS G. RAVELING*
Canadian Wildlife Service,
Winnipeg, Manitoba, Canada R3T 2N6

References and Notes

1. H. A. Hochbaum, *Travels and Traditions of Waterfowl* (Univ. of Minnesota Press, Minneapolis, 1955), pp. 112 and 113, 132 and 133; J. Dorst, *The Migrations of Birds* (Houghton Mifflin, Boston, 1962), pp. 239 and 240.

→ G. A. Sherwood, *J. Wildl. Manage.* **30**, 853 (1966).

3. H. C. Hanson, *Ill. Nat. Hist. Surv. Biol. Notes* **49**, 1 (1962).
4. ______, *The Giant Canada Goose* (Southern Illinois Univ. Press, Carbondale, 1965), pp. 97–99; N. A. Gulden and L. L. Johnson, in *Canada Goose Management*, R. L. Hine and C. Schoenfeld, Eds. (Dembar Educational Research Service, Madison, Wis., 1968), p. 59.
5. T. Sterling and A. Dzubin, *Trans. North Am. Wildl. Nat. Resour. Conf.* **32**, 355 (1967).
6. D. G. Raveling, in *Canada Goose Management*, R. L. Hine and C. Schoenfeld, Eds. (Dembar Educational Research Service, Madison, Wis., 1968), p. → *J. Wildl. Manage.* **33**, 304 and 330 (1969); *Auk* **86**, 671 (1969); *Behaviour* **37**, 291 (1970).

→ C. S. Williams and W. H. Marshall, *J. Wildl. Manage.* **2**, 17 (1938); A. W. Miller and B. D. Collins, *Calif. Fish Game* **39**, 385 (19 → G. K. Brakhage, *J. Wildl. Manage.* **29**, 751 (1965).

8. R. W. Vaught and L. M. Kirsch, *Canada Geese of the Eastern Prairie Population* (Missouri Department of Conservation Technical Bulletin No. 3, 1966), p. 45.
9. H. Fischer, *Z. Tierpsychol.* **22**, 247 (1965).
10. J. Delacour, *The Waterfowl of the World* (Country Life, London, 1954), vol. 1, pp. 150–178.
11. I thank the P. D. Curry and A. J. Vincent families for permission to study on their property; many personnel of the Manitoba Department of Mines, Energy, and Natural Resources and the Minnesota Department of Natural Resources for assistance in the field; M. R. Petersen for assistance in preparation and analysis of data.

* Present address: Division of Wildlife and Fisheries Biology, University of California, Davis 95616.

9 January 1976; revised 27 April 1976

Mevalonate Metabolism: Role of Kidneys

Abstract. *More than one-half of the amount of mevalonate that is metabolized by pathways not leading to sterols is accounted for by the action of the kidneys. Conversion of mevalonate in vivo to squalene and sterols in the kidneys is confined almost entirely to the proximal and distal convoluted tubules in the cortex. More sterol than squalene is synthesized from mevalonate not only in the liver but also in the kidney.*

We have reported that mevalonate is metabolized in the rat and man not only for the synthesis of polyprenyl substances and sterols, but also on a pathway not leading to sterols (*1, 2*). In order to explain our observations (transfer of C-2 of mevalonate to palmitate and stearate, and the appearance of $^{14}CO_2$ in the breath of animals and man within 1 minute after injection of [5-^{14}C]mevalonate) we proposed a hypothetical metabolic pathway whereby an intermediate derived from mevalonate (possibly 3,3-dimethylallyl pyrophosphate) was diverted from the main sterol-synthesizing reaction sequence via *trans*-3-methylglutaconyl-CoA to ketone bodies and acetyl-CoA in ketogenic organs, the liver, intestine, and kidneys. This metabolic pathway was termed the "*trans*-methylglutaconate shunt" of mevalonate metabolism (*1*).

Because of the known avid utilization of mevalonate by the kidneys for the synthesis of squalene and sterols (*2–5*), and because of its known function in ketogenesis (*6*), we have examined by experiments in vivo the possible role of the kidneys in this "shunt" activity and the

Table 1. $^{14}CO_2$ in breath of paired control and nephrectomized rats exhaled in 2.5 hours after injection of 2 μmole of *RS*-[5-^{14}C]-mevalonate (MVA).

Experiment	$^{14}CO_2$ (percent of *R*-MVA dose)		$\frac{B}{A} \times 100$
	A*	B†	
1	6.08	2.64	43.4
2	6.31	3.02	47.8
3	6.76	2.58	38.2
4	17.88	5.60	31.4
5	14.35	6.28	43.8

*Sham-operated controls; mean body weight, 284 ± 14 g. †Bilaterally nephrectomized; mean body weight, 286 ± 15 g.