curve for the rabbit vagus reported by Keynes and Ritchie (*2*). Nonmyelinated nerve fibers that arise in the dorsal root ganglia and travel in the saphenous nerve of the cat have a distribution of diameters essentially the same as that for the vagus (*15*).

The small filament shown in Fig. 1B, occupied by 1577 axons, together with Schwann cells, empty spaces, and collagen, is equivalent in cross-sectional area to one large myelinated fiber about 15 μm in diameter. Assuming, in such a fiber, 100 Schwann cell layers totaling 1 μm thick, we may compare the two kinds of fibers. In the olfactory nerve, the relative amount of axon surface is more than three times the Schwann cell surface, whereas in the myelinated fibers, conversely, the area of Schwann cell membranes is at least 100 times the axon surface, but axon volume is five times the Schwann cell volume. The ratio of axon membrane surface to Schwann cell membrane surface is over 400 times as great in the olfactory nerve filament as it is in the myelinated fiber. The axons provide 80 percent of the cell membranes in the olfactory nerve, but only 1 percent in the hypothetical A fiber chosen as an example. The ratio of surface to volume for the Schwann cells is nearly ten times as great in the myelinated fiber as in the olfactory nerve filament, but the corresponding ratio for the axons is 50 times greater, in favor of the nonmyelinated filament. The entire olfactory nerve has about the same cross-sectional area (about 1.54 mm^2, Fig. 1A) as a squid giant axon. The ratio of axon membrane to axon volume in the 10^7 fibers of the garfish olfactory nerve is about 5400 times as great as that in the single giant axon.

Relationships of this sort may be helpful in allocating to specific compartments substances determined to be present in nerve. Of particular interest may be the comparison of materials likely to be found mainly in axon membrane where they may relate to the process of impulse conduction, in contrast to Schwann cell membrane where they will have less direct relevance to the molecular mechanism of nerve excitation. For some problems in axonology, therefore, the olfactory nerve of the garfish may be even more useful than the giant axon of the squid. The elucidation of metabolic phenomena and their correlation with electrophysiological events may perhaps be made more easily with the help of this large nerve, composed of a homogeneous population of small fibers having slow conduction velocity, short-length impulses, and extensive surface relative to volume.

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10. The nerve functioned satisfactorily for several hours in a physiological solution containing in final concentration: 125 m*M* NaCl, 3.5 m*M* KCl, 3.5 m*M* $CaCl_2$. Survival during stimulation for a day or more was favored by addition of sucrose (60 mmole/liter) to increase osmotic pressure and prevent swelling during prolonged experiments, of glucose (24 mmole/liter) as energy source, of phosphate buffer (1 mmole/liter), and, when 95 percent O_2 and 5 percent CO_2 was used as the gas phase, of $NaHCO_3$ (10 mmole/liter).
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15 January 1971; revised 4 Februray 1971 ■

DDE Residues and Eggshell Changes in Alaskan Falcons and Hawks

Abstract. *Eggshell thickness after exposure to DDT was reduced by 21.7 percent in Alaskan tundra peregrines, by 16.8 percent in taiga peregrines, by 7.5 percent in Aleutian peregrines, by 3.3 percent in rough-legged hawks, and not at all in gyrfalcons. Tundra peregrine eggs contain an average of 889 parts of DDE per million (lipid basis); taiga peregrine eggs contain 673 parts per million; Aleutian peregrine eggs contain 167 parts per million; rough-legged hawk eggs contain 22.5 parts per million; and gyrfalcon eggs contain 3.88 parts per million. These changes in eggshell thickness and the pesticide residues reflect different degrees of exposure to contamination. There is a highly significant negative correlation between shell thickness and DDE content in peregrine eggs. Tundra and taiga peregrines have fledged progressively fewer young each year since 1966.*

During 1967 to 1970 we studied organochlorine contamination in Alaskan breeding populations of raptors, especially the peregrine falcon *Falco peregrinus*, which has experienced serious population declines on two continents since the late 1940's (*1*). Work along the Yukon River in 1966 revealed that the peregrines there were already heavily contaminated with organochlorine residues, mostly 2,2-bis(*p*-chlorophenyl) 1,1-dichloroethylene (DDE), although the number of breeding pairs and reproductive output remained within historically predictable limits (*2*).

In 1967, Ratcliffe demonstrated a close correspondence in time and space between sudden, dramatic changes in eggshell weight and exposure to persistent organochlorine pesticides in three declining species of British raptors (*3*). The DDE has become increasingly implicated as the main organochlorine compound causing shell thinning and population decline (*4*, *5*), but the polychlorinated biphenyls may also be involved (*6*).

We now report data on eggs from three geographic populations of *Falco peregrinus*: (i) on Amchitka Island in the Aleutians, (ii) along the Yukon River in the interior taiga, and (iii) along the Colville River in the foothill tundra of the Arctic Slope. For com-

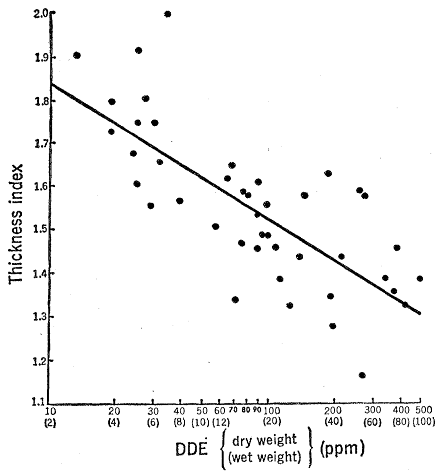

Fig. 1. Relation between shell thickness index (weight in milligrams divided by length times width in millimeters) and DDE residues in eggs of Alaskan peregrine falcons. The scale for wet weight has been constructed by dividing the measured dry weight values by 5. A sample of seven eggs had an average water content of 80 percent. If the regression were linear over the entire range from 0 to 500 ppm, then the y-intercept should correspond to indices of 1.85 to 1.90 prior to exposure to pesticides. The relationship probably breaks from linearity at both low and high residue values, hence the lack of correspondence. $N = 43$; $y = 2.15 - 0.316x$; $r = -0.745$; and $P < .001$.

parison we have examined eggs from gyrfalcons *Falco rusticolus* on Seward Peninsula and from rough-legged hawks *Buteo lagopus* nesting along the Colville River (*7*).

Because of their different food habits and migratory movements, each of these raptor populations is exposed to a different degree of chemical hazards. The peregrine is a bird-eater, feeding heavily on migrant waterfowl, shorebirds, and passerines, species which are primary or secondary predators and which carry significant amounts of pesticide residues in their bodies (*2*). The tundra and taiga peregrines are long-distance migrants, which breed in the Far North during the months of May through August but winter mainly south of the United States, as far as Argentina (*8*). Their annual migrations bring them in contact with some of the most polluted areas in the Western Hemisphere. The Aleutian peregrines are resident in the islands, and their prey derives from a marine food chain, as they feed on alcids and other seabirds, most of which remain in the Bering Sea or North Pacific the year round and which carry remarkably low amounts of DDE residues (*9*). The gyrfalcon is resident in arctic and subarctic regions, although local, seasonal shifts in populations do occur. It feeds on ptarmigan, *Lagopus lagopus* and *L. mutus*, which are resident, herbivorous gamebirds only one trophic level removed from the primary production of the tundra vegetation. The rough-legged hawk feeds chiefly on herbivorous lemmings and voles. It breeds sympatrically with the peregrine in the Far North, often nesting on the same cliffs, and migrates south in fall; but most of the wintering birds remain in southern Canada and in the northern tier of the contiguous United States (*10*).

Changes in eggshell thickness and residues of DDE (*11*) in egg contents reflect these differences among the sampled populations (Table 1). The peregrines have experienced large reductions in eggshell thickness since the beginning of widespread DDT applications in 1946; the gyrfalcons and rough-legged hawks have not. The tundra and taiga peregrines now lay eggs with shells as thin as those associated with the decimated populations of Great Britain, California, and the eastern United States (*3–5*).

Our findings in Table 1 lead to the same conclusion as those for 17 species of British birds (*5*)—with but two or three exceptions, significant reductions in shell thickness since 1946 are associated with high amounts of organochlorine residues in egg contents, and those species that lay thin-shelled eggs are top predators at the ends of long food chains, mostly bird- and fish-eaters, or else their food has been highly contaminated by special uses of organochlorine poisons, such as dieldrin in sheep dips in the case of Scottish golden eagles *Aquila chrysaetos* (*12*).

There is a highly significant negative correlation between shell thickness and parts of DDE per million in egg contents for Alaskan peregrines (Fig. 1) (*13*). Our results substantiate Ratcliffe's conclusion for British peregrine eggs (*3*), as well as similar findings for the eggs of prairie falcons *Falco mexicanus* from Colorado and Alberta (*14*).

Our fieldwork convinces us that there has been no decrease in the numbers of gyrfalcons and rough-legged hawks in northern Alaska since the first studies in the 1950's (*15, 16*). The peregrine warrants closer scrutiny, as the Alaskan falcons clearly have experienced a chronic, altered reproductive physiology, which—in its extreme form—has been responsible for the extirpation of this species over many parts of its once nearly worldwide range. The number of breeding pairs in the Colville and Yukon areas remained steady through 1969 (Table 2), but the trend in production of young

Table 1. Eggshell thickness index (weight in milligrams divided by length times width in millimeters) and DDE residues (lipid basis) in egg content for five populations of Alaskan raptors. Data for shell thickness prior to 1947 from D. W. Anderson and J. J. Hickey. Their tundra peregrine eggs were from northern Alaska and the Northwest Territories, those of taiga peregrines came from interior Alaska, those of maritime peregrines came from Forrester Island, those of rough-legged hawks came from various sites in Alaska, and those of gyrfalcons came from Alaska and the Northwest Territories. Statistical significance was determined by Student's t-test. N.S., not significant.

Population	Thickness index				DDE content		
	No.	Range	Mean	P	No.	Range (ppm)	Mean (ppm)
Peregrines							
Tundra < 1947	18	1.62–2.31	1.89	< .001			
Colville 1967–69	23	1.16–1.73	1.48		19	159–3130	889
Taiga < 1947	20	1.61–2.04	1.79*	< .001			
Yukon and interior 1968–69	14	1.32–1.64	1.48		14	210–1343	673
Maritime < 1947	30	1.72–2.16	1.88	< .02			
Amchitka 1969–70	11	1.46–1.99	1.73		11	97–420	167
Gyrfalcons							
< 1947	25	1.89–2.60	2.26	N.S.			
Seward Peninsula 1968–69	12	1.90–2.53	2.25		13	0–20.3	3.88
Rough-legged hawks							
< 1947	41	1.81–2.47	2.15	> .05			
Colville 1967–69	16	1.78–2.28	2.08		25	2.20–109.0	22.5

* This mean is probably too low as all other known samples of peregrine eggs prior to 1947 average between 1.84 and 1.99 (*3–5, 20*).

Table 2. Reproductive performance of Alaskan peregrines.

Year	Pairs (No.)	Unproductive pairs (No.)	Eggs or downies (No./laying female)	Fledglings (No./pair)	Young probably fledged (No.)
		Yukon River (275 km)			
1951*	16–19	7		1.05–1.25	20
1966	17	3	3.09	1.80	30
1967	15			1.40	21–23
1968	17	8	3.80	0.93	16
		Colville River (293 km)			
1952*	32	11	3.18	1.40	44
1967	27	9	2.22	1.26	34
1968	32	16	2.78	1.06	34
1969	33	20	2.92	0.79	26 or less

* See (*16*).

has been downward since 1966 and appears to be associated mainly with an increase in the number of pairs that fail completely, rather than with a decrease in clutch size or reduced hatchability of eggs. This pattern of failure fits the thin-eggshell syndrome, as a heavily contaminated female is likely to produce an entire clutch of thin-shelled eggs, all of which break, whereas a less contaminated female will produce eggs with shells thick enough to last through incubation.

The Colville peregrines did not do well in 1970. On a stretch of the river where 18 or 19 pairs could be expected to start the season, only five pairs with ten young, 2.5 to 3 weeks old, were present in late July, or an indicated production of not more than 0.56 young per known aerie; 72 percent of the aeries failed. The situation was slightly better in interior Alaska. On a stretch of the Tanana River where 13 to 14 aeries were active in the 1960's, a survey in early July revealed seven pairs with 20 young 2 to 3 weeks old (*17*). On a stretch of the Yukon River where historically eight to nine pairs have bred, eight pairs began the 1970 season, four failed completely, but the remainder fledged ten young. A late-season check along 275 km revealed seven successful pairs with 18 nearly fledged young (*18*), indicating that 60 percent of the known aeries failed.

The occurrence of thin-shelled eggs and high pesticide residues in Alaskan peregrines seems paradoxical to some people, because breeding populations have held steady until now and productivity has remained—if not normal—at least within limits sufficient for adult replacement at the aeries. The few eggs we have early in the pesticide era indicate that thin shells have characterized the Colville population for about 20 years. Three eggs collected by C. M. White in 1964 have shell indices around 1.4, and three collected by J. W. Bee on Umiat Mountain in 1952 are around 1.45 to 1.5. It seems likely that the arctic peregrines have maintained their numbers with a marginal reproductive physiology since the early 1950's. We feel they have done so only because they migrate to breed in regions where there is relatively little residue buildup in their food chains; thus, organochlorine residues in the falcons have remained below the threshold that initiates population decline, although many individual females have no doubt been rendered incapable of reproducing. Our observations in 1970 indicate that this threshold has now been exceeded and that recruitment no longer equals the adult mortality rate, as pairs have begun to disappear from their historic nesting crags on the Colville and Yukon rivers, just as they did 20 years ago along the Hudson and Susquehanna (*19*).

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7. Peregrine eggs from the Yukon and Colville rivers and the rough-legged hawk eggs were collected during studies supported by the Arctic Institute of North America with funds from ONR, T. J. Cade, principal investigator. We thank J. H. Enderson, J. R. Haugh, W. R. Spofford, and S. A. Temple for help in the field. C. M. White collected the eggs from Amchitka during studies under AEC contract AT (26-1)-171 for Battelle Memorial Institute, Columbus, Ohio, F. S. L. Williamson, principal investigator. D. G. Roseneau collected the gyrfalcon eggs during work for the Alaska Department of Fish and Game, R. B. Weeden, project director. In most cases the eggs were blown by routine oological methods in the field, and the egg contents were immediately preserved in 10 percent formalin; in a few instances intact eggs were shipped from the field to Cornell University where residue analyses were performed.
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6 October 1970; revised 25 November 1970