Invited Commentary: Fifty Years of Raptor Research

Author: Ian Newton

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INVITED COMMENTARY: FIFTY YEARS OF RAPTOR RESEARCH

TRANSCRIPT OF A PLENARY ADDRESS PRESENTED AT THE RAPTOR RESEARCH FOUNDATION 50-YEAR ANNIVERSARY CONFERENCE, CAPE MAY, NEW JERSEY, 17 OCTOBER 2016

IAN NEWTON[1]

Centre for Ecology and Hydrology, Benson Lane, Crowmarsh Gifford, Wallingford, Oxon OX0 8BB, U.K.

ABSTRACT.—This review examines the main developments that have occurred over the past 50 years in our understanding of three aspects of raptor biology: (1) natural factors that limit breeding densities; (2) influences of toxic chemicals; and (3) movements and migrations. Early evidence indicated that raptor breeding densities were limited naturally by the availability of either prey or nest sites, whichever was in shortest supply in the area concerned. More recent evidence has shown that predation can have additional influence, with larger raptors and owls limiting the numbers of smaller ones to below what food or nest sites would permit. In addition, it has become apparent that some migratory raptors, like other migratory birds, can be limited in their migration and wintering areas to levels below those that conditions in breeding areas would permit. As many raptor populations have recovered from the effects of organochlorine pesticides, attention has switched to other limiting agents, including lead (from ammunition), which is currently preventing California Condors (*Gymnogyps californianus*) from establishing self-sustaining populations in the wild, and anti-inflammatory veterinary drugs, which have caused massive declines in Asia vultures (*Gyps* spp.). The development of radio-tracking enabled studies of the local movements of individual raptors, providing new information on territories and ranging behavior, while satellite-based tracking has revealed the migration routes, wintering areas, and behavior of hundreds of individual birds.

KEY WORDS: *breeding density*; *contaminant*; *migration*; *movement*; *population*; *raptors.*

COMENTARIO INVITADO: CINCUENTA AÑOS DE INVESTIGACIÓN DE RAPACES

RESUMEN.—Este análisis examina los principales progresos que han ocurrido durante los últimos 50 años en nuestro conocimiento acerca de tres aspectos de la biología de las aves rapaces: (1) los factores naturales que limitan las densidades de cría; (2) la influencia de químicos tóxicos; y (3) los movimientos y las migraciones. Las primeras pruebas indicaban que las densidades de aves rapaces reproductoras estaban limitadas de forma natural por la disponibilidad de presas o de lugares de nidificación, cualquiera que se encontrase en menor medida en el área de estudio. Evidencias más recientes han demostrado que la depredación puede tener una influencia adicional, siendo las aves rapaces de mayor tamaño y los búhos los que limiten el número de rapaces más pequeñas a niveles menores de lo que el alimento o los lugares de nidificación permitirían. Además, se ha demostrado que algunas especies de rapaces migratorias, como en otras aves migratorias, pueden estar limitadas en sus áreas de migración e invernada a niveles menores de lo que permitirían las condiciones en las áreas de cría. A medida que las poblaciones de rapaces se fueron recuperando de los impactos de pesticidas organoclorados, la atención ha recaído sobre otros agentes limitantes, incluyendo el plomo (proveniente de municiones), que está impidiendo actualmente el establecimiento de poblaciones sostenibles por sí mismas de *Gymnogyps californianus* en estado silvestre, y los medicamentos antiinflamatorios veterinarios, los cuales han causado graves declives en las poblaciones

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[1] Email address: ine@ceh.ac.uk

de buitres asiáticos. El desarrollo del seguimiento por radio-tracking ha permitido el estudio de los movimientos locales a nivel individual en rapaces, aportando nueva información sobre los territorios y el uso del espacio, mientras que el seguimiento vía satélite ha mostrado las rutas migratorias, las áreas de invernada y el comportamiento de cientos de aves a nivel individual.

[Traducción del equipo editorial]

When I first went to a Raptor Research Foundation (RRF) meeting, held at Boise, Idaho, in 1975, I was amazed at the sheer number of raptor enthusiasts gathered at that meeting. It was like today, hundreds of people—amateurs and professionals alike—united in a common interest. These were exciting times, for we were in the midst of the organochlorine era, with DDT and similar pesticides. Peregrine Falcons (*Falco peregrinus*), Bald Eagles (*Haliaeetus leucocephalus*), Ospreys (*Pandion haliaetus*) and other raptors were in headlong decline, and captive breeding was just getting off the ground. Raptors had been so little studied that we knew little of relevance about most of the species we were trying to protect. My talk today will be very much a personal view, picking out some of what I think are the major advances in raptor research and conservation that have occurred over the past 50 years, concentrating on three main aspects: (1) the natural factors that limit raptor populations, (2) some of the unnatural factors that limit raptor numbers, namely pesticides and other toxic chemicals, (3) movements and migratory behavior.

LIMITATION OF BREEDING DENSITIES

Population limitation in raptors is an issue that concerns us all. For if we are to conserve raptors, we must understand the factors that influence their numbers. Fifty years ago, the evidence that food supply could affect raptor nesting densities was of three kinds. First, regional variations in breeding density of particular species were related to regional variations in their food supplies. Secondly, in other species, annual fluctuations in densities were correlated with annual fluctuations in their prey. This was especially obvious in species that fed on cyclic prey, whether the 3–5-yr cycles of rodents or the 10-yr cycles of hares and game birds. Finally, exceptionally high densities in raptors, found in a few places, were associated with an exceptional food situation. One of the most extreme, found in the 1960s by Galushin (1971), was the average of nearly 20 raptor pairs per km^2, mainly Black Kites (*Milvus migrans*), found throughout the city of Delhi in India, associated with a huge amount of food within the city: garbage, carcasses of animals on roads, and discarded waste from slaughter houses, enough for nearly 3000 pairs in 150 km^2 of crowded city.

Years ago when I was studying Eurasian Sparrowhawks (*Accipiter nisus*), it soon became apparent that the nests of different pairs were regularly spaced through forest areas, reflecting the territorial behavior of the birds themselves (Newton et al. 1986). To get a measure of spacing, I took the nearest-neighbor distances from every nest, and used the average as a measure of nest spacing in the area as a whole. In different areas, spacing differed. In some areas, nests averaged about 0.5 km apart, and in others they were more than 2 km apart, giving more than a 16-fold variation in density between areas, but with nests always regularly spaced. Such patterns proved to be consistent from year to year, and further work revealed that densities were related to food supply, the abundance of small birds in the areas concerned. In Figure 1, the mean nearest-neighbor distance of sparrowhawks in different areas is shown in relation to an index of small bird prey, as obtained by point counts. Over this range, as prey density increased in different areas, mean nearest neighbor distances of sparrowhawks declined: the birds nested closer together in areas where their prey were most numerous or had the greatest biomass. Within suitable forest nesting habitat, it seemed that prey supply influenced densities. Similar relationships between densities and food supply emerged in many other raptors studied over the years, including Golden Eagles (*Aquila chrysaetos*), Common Buzzards (*Buteo buteo*), and peregrines, all of which took a wide range of prey species and, despite the regional differences, showed fairly consistent densities from year to year (Newton 1979, Ratcliffe 1993, Watson 2010). Populations remained relatively stable over long periods of years.

Other raptors and owls, which depended on a very limited number of cyclically fluctuating prey, varied from year to year in line with their prey. For example, in an area of Finland, the densities of Short-eared Owls (*Asio flammeus*) over an 11-yr

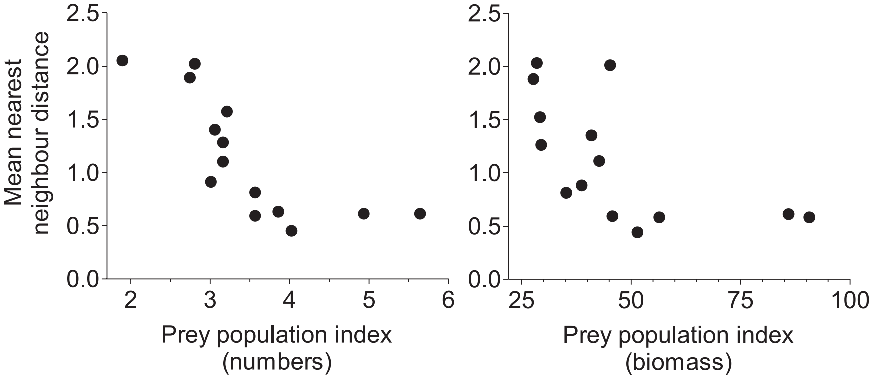

Figure 1. Spacing of sparrowhawk nests (shown by mean nearest neighbor distance) in relation to prey density (as indexed by point counts of all prey species together, expressed as numbers and biomass). From Newton et al. 1986.

period varied in line with the densities of voles (Fig. 2; Korpimäki and Norrdahl 1991). The owls were absent from the area in winter, and on their return in spring, they settled at densities in line with the prey supply. The owls themselves apparently moved around from year to year, seeking out areas with abundant voles. This kind of pattern has been found in many raptors and owls that feed on greatly fluctuating prey, giving another line of evidence that breeding densities of raptors and owls can be influenced by food supply (Newton 2002).

However, we have all met situations where prey are present in abundance, but raptor breeding densities are low because of scarcity of suitable nest sites. This is especially obvious in the case of cliff-nesters such as the peregrine in some areas, or cavity-nesters such as the Eurasian Kestrel (*Falco tinnunculus*) or Barn Owl (*Tyto alba*). In such situations, the addition of nest sites can lead to an increase in nesting density, as is obvious now in many studies of different owls and raptors, which will accept nest-boxes in place of natural tree cavities. It is also obvious in Ospreys, eagles, and others that will accept platforms or power poles in places they could not otherwise nest, thereby raising the general density until it is more in line with the available food supply.

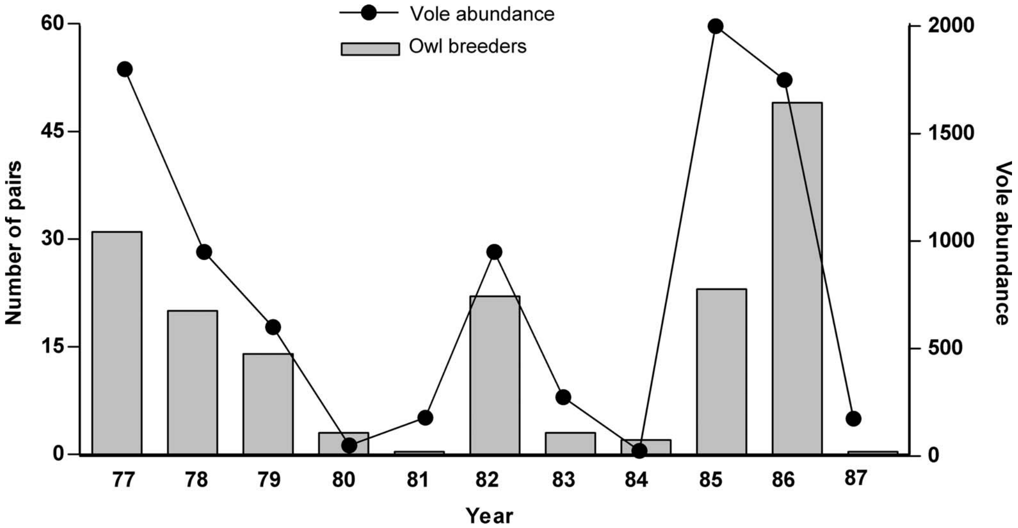

Figure 2. Numbers of Short-eared Owls (*Asio flammeus*) breeding in an area of Finland each year in relation to the abundance of *Microtus* voles. Adapted from Korpimäki and Norrdahl 1991.

The conclusion emerged, then, that within suitable habitat, the breeding densities of raptors were naturally limited by either food or nest sites, whichever was in shortest supply in the area concerned (Newton 1979). It was, of course, accepted that human impacts could reduce numbers below this natural level, for example, by direct killing or pesticide effects. This conclusion put the emphasis on the breeding area, and could apply to resident species present in an area year-round or to summer visitors that moved in to breed. However, many raptors are migratory, at least in some parts of their range, so in theory their numbers might be limited either in breeding areas, as I have explained, or in their migration or wintering areas. One could imagine a situation in which birds were so strongly limited in wintering areas that they might never fill the breeding habitat to capacity, whatever the food and nest sites available there (see below).

A second, more recent, addition to ideas on population limitation concerns predation. In recent decades, it has become increasingly apparent that big raptor species can control the numbers of small ones. This so-called intra-guild predation has now been well documented, especially in Europe where many big raptors have recovered in numbers in recent years, revealing their previously unsuspected impacts on smaller raptors. Typically, the bigger raptor limits the distribution of the smaller raptor to only some parts of the habitat it might otherwise occupy. We had hints of this in the past, but in recent years many more well-documented examples have come to light (Table 1; Sergio et al. 2003, Sergio and Hiraldo 2008). Some predators, such as Northern Goshawk (*Accipiter gentilis*) and Eurasian Eagle-Owl (*Bubo bubo*), seem to limit quite a range of species to below the level that food and nest-sites would permit. In one area or another, the goshawk has been found to limit the numbers of at least eight other predatory species, varying in size from Eurasian Hobby (*Falco subbuteo*; 200 g) to buzzard (1 kg); while the eagle-owl has been found to limit at least seven species, from Tawny Owl (*Strix aluco*) to Ural Owl (*S. uralensis*) and Booted Eagle (*Hieraaetus pennatus*), having the advantage of being able to operate at night. In each case, as the bigger species moved in, the smaller species disappeared, at least from parts of the habitat.

For a more specific example, as goshawks colonized Kielder Forest in northern England, eventually stabilizing at around 20 pairs, the once-abundant kestrels declined catastrophically (Petty et al. 2003). Each spring goshawks were estimated (from prey remains) to remove an average of 115 kestrels from this area, far more than the number that normally nested there. Evidently, kestrels were removed as they settled the area in spring, and as one lot was removed by goshawks, others moved in to replace them, some of which were also removed, and so on. By this successive removal of newly arrived migrants, goshawks had a far greater impact on kestrels than if they had just removed the local breeding pairs. The rise of goshawks in this area was also associated with declines in the local populations of Merlins (*Falco columbarius*) and Short-eared Owls, but on the other hand, goshawks had no detectable impact on nocturnal species such as Tawny Owls and Long-eared Owls (*Asio otus*).

But the goshawk is itself not immune to predation. The eagle-owl is a bigger and stronger version of the North American Great Horned Owl (*Bubo virginianus*), and within 12 yr of eagle-owls recolonizing a German area, goshawks had declined to a third of their former level, almost all their original nests had been taken over by owls, and those goshawks that remained seldom produced young, even though no goshawk nested anywhere near its major predator (Busche et al. 2005).

Table 1. Examples of intraguild predation in which the predator species has been found to reduce or limit the breeding density of the prey species. Data from Sergio and Hiraldo 2008.

PREDATOR SPECIES	PREY SPECIES
Northern Goshawk (*Accipiter gentilis*)	Eurasian Kestrel (*Falco tinnunculus*); Eurasian Hobby (*F. subbuteo*); Merlin (*F. columbarius*); Black Kite (*Milvus migrans*); Red Kite (*M. milvus*); Eurasian Sparrowhawk (*Accipiter nisus*); Short-eared Owl (*Asio flammeus*); Carrion Crow (*Corvus corone*)
Golden Eagle (*Aquila chrysaetos*)	Peregrine Falcon (*F. peregrinus*), Common Buzzard (*Buteo buteo*)
Eurasian Eagle-Owl (*Bubo bubo*)	Northern Goshawk; Black Kite; Booted Eagle (*Hieraaetus pennatus*), Common Buzzard; Tawny Owl (*Strix aluco*); Ural Owl (*Strix uralensis*)

Sometimes the effect of intraguild predation is passed down the food chain. The conclusion of a study by Sergio et al. (2007) from northern Italy was that eagle-owls limit the numbers of medium-sized Tawny Owls, which in turn limit Eurasian Scops-Owls (*Otus scops*) and other small owls, to produce a "trophic cascade." The small owls are too small to be of interest to eagle-owls. So in comparing different areas: some had abundant eagle-owls, hardly any Tawny Owls and very abundant small owls, while others had no eagle-owls, lots of Tawny Owls, and very few smaller owls. The top predators generally increased the abundance and diversity of those species two steps below them in the food chain, by removing the intermediate predator. Another example involves the eagle-owl, the somewhat smaller Ural Owl, and the much smaller Boreal Owl (*Aegolius funereus*) in Finland (Hakkarainen and Korpimäki 1996). Studies elsewhere have shown that Ural Owls are even more significant predators of Tawny Owls and can totally exclude them from some areas, and the same holds for the effects of Tawny Owls on Boreal Owls (Vrezec and Tome 2004). Big species reduce the breeding densities of smaller ones either by direct predation (killing and eating them), or by deterring small species from settling in places otherwise suitable for them. So predation is clearly another widespread factor which can limit the numbers and distributions of many species of raptors and owls.

All the examples refer to breeding densities, but winter predation might have similar impacts. Effects have been revealed mainly because larger raptors have been released from whatever limiting factor was previously holding them down, whether human persecution, toxic chemicals, or some other unknown factor. It raises the possibility that environments rich in small raptors, such as American Kestrels (*Falco sparverius*) or Sharp-shinned Hawks (*Accipiter striatus*), which many of us remember from years ago, may have resulted from the human-induced scarcity of their predators. Parallel intraguild predation, with effects down the food chain, has been documented in the context of mammalian predators.

Toxic Chemicals

Of all the human-made chemicals that have reached the natural environment, it is arguably the organochlorines that have so far had the most wide-scale impacts on raptor populations. For more than 30 yr, these chemicals dominated or stimulated research on raptors, for a time figuring prominently at every meeting of the RRF. For this reason, and the lessons revealed, I think it is worth rerunning the story. Organochlorines included DDT, lindane, and other more toxic cyclodienes, such as aldrin, dieldrin, and heptachlor. They were important to wildlife because of a unique combination of extreme properties: besides being toxic, they were (1) chemically extremely stable (persisting unchanged for years in the environment); (2) fat-soluble (accumulating in animal bodies, and passing from prey to predator); (3) capable at very low concentrations of having sublethal effects on reproduction; (4) capable of being dispersed widely in animal bodies, air, and water, reaching remote regions, far from where they were used or manufactured. They soon became globally distributed.

As we now know, different organochlorines affected raptors in different ways (Fig. 3): DDT is not especially toxic to birds, and its main effects are on breeding. Once in the bird's body, most of the DDT is rapidly converted to a much more stable metabolite, DDE, which forms the bulk of the residue detected in bird eggs and carcasses. At sublethal level, DDE reduces the availability of calcium carbonate during eggshell formation, so that the eggs are thin-shelled and break when the female treads or sits on them. Alternatively, some thin-shelled eggs may survive incubation, but the embryo dies from dehydration caused by excess water loss through a thinned shell. If the reduction in the average breeding rate of individuals resulting from these two effects is sufficiently marked, it leads to population decline, because reproduction is no longer sufficient to offset the usual annual mortality.

Other organochlorines, notably the cyclodienes (aldrin and dieldrin, together denoted as HEOD), are several hundred times more toxic to birds than is DDT or DDE (Hudson et al. 1984). These chemicals act mainly by killing birds outright, increasing mortality above the natural level, so as to cause rapid population decline (Fig. 3). DDE at very high level can also kill birds, and HEOD can also affect reproduction, but for practical purposes, at the concentrations normally found, there were two main mechanisms.

The relative importance of these two mechanisms varied between regions: in North America, DDT seemed mainly responsible for declines in peregrines and others. In Britain/western Europe, more

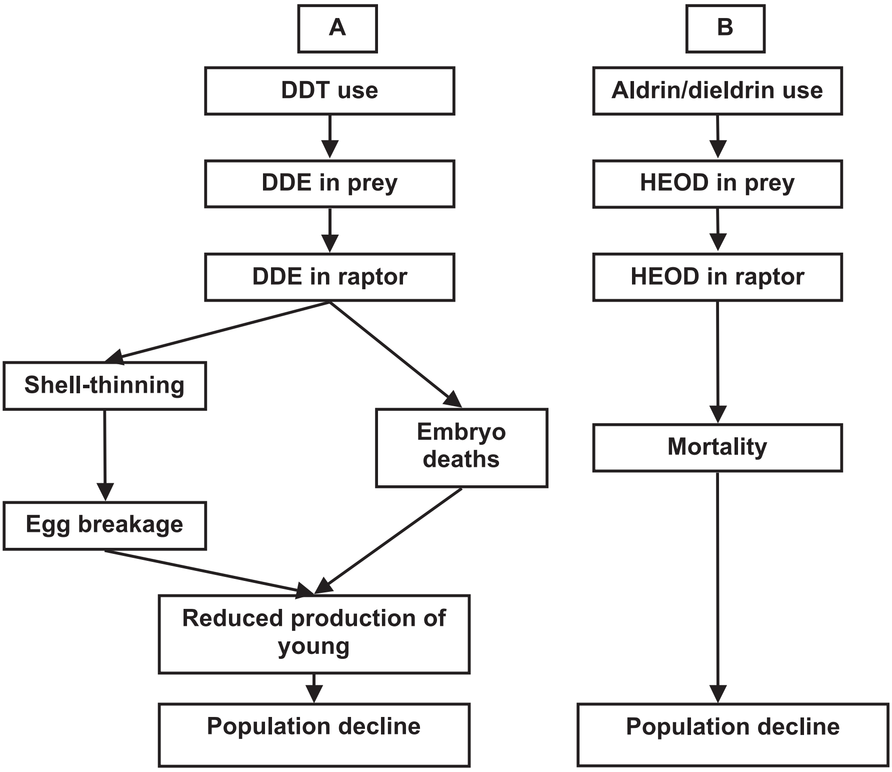

Figure 3. Modes of action of DDE (from the insecticide DDT) and HEOD (from aldrin and dieldrin) on raptor populations. From Newton 1986.

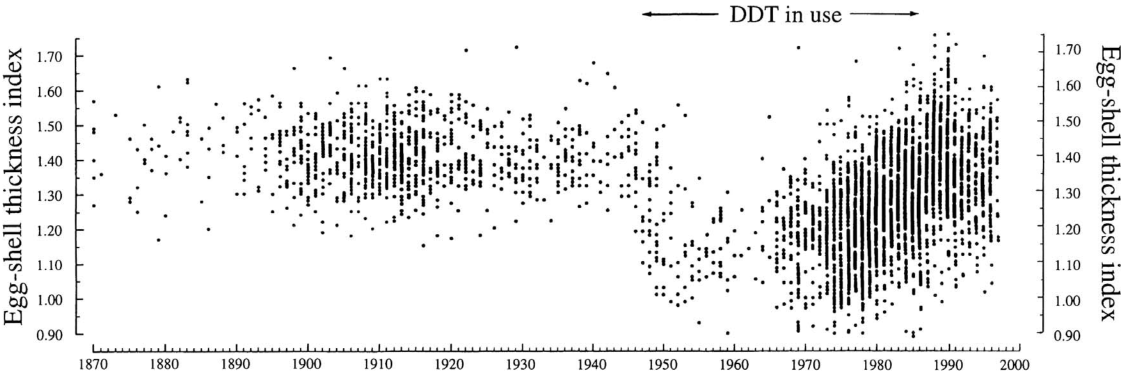

Figure 4. Shell-thickness index of Eurasian Sparrowhawks (*Accipiter nisus*) in Britain, 1870–1997; the research program came to an end in 1998. Shell-thinning became apparent very quickly from 1947, following the widespread introduction of DDT in agriculture. The problem improved from the 1970s, following progressive restrictions in the use of the chemical, which was banned altogether from 1986. Each dot represents the mean shell index of a clutch (or part-clutch), and more than 2000 clutches are represented from all regions of Britain. Shell index was measured as shell weight (mg)/ shell length × breadth (mm). Adapted from Newton 1986.

dieldrin was used, and increased mortality was the main factor causing declines in populations, many of which crashed within 2–3 yr of dieldrin being introduced. Some combination of the two mechanisms may have caused all the population declines recorded at this time, but with declines being most rapid in populations most heavily exposed to dieldrin and other cyclodienes. It took 20 yr to work out these different mechanisms.

One of the most important discoveries was eggshell thinning, first documented by Derek Ratcliffe (1967, 1970) who used eggshells in museums and private collections to date the timing of shell-thinning in raptors, finding it fitted the introduction of DDT in agriculture. Figure 4 shows the pattern of eggshell thinning in Britain, based on eggs examined by Derek Ratcliffe and myself. Eggs were available over the period 1870–2000. Shell-thinning became first apparent in the late 1940s (specifically 1947) immediately following the introduction of DDT in agriculture. Almost all the eggs examined over the next 15–20 yr were well-thinned, and then, as DDT was progressively phased out of use, sparrowhawk eggshells gradually recovered. These historical data for various species formed one line of evidence implicating DDT. After this initial discovery, it became possible to examine the shells of individual eggs, collected from concurrent wild nests, and relate the level of thinning to the concentration of organochlorines within the egg (presumably reflecting the concentration in the female that laid the egg). For several species, the relationship emerged as linear, with DDE on log scale. Critically, there was also some experimental work, in which captive raptors fed DDE then laid thin-shelled eggs, as found at the U.S. Fish and Wildlife Lab at Patuxent and at Cornell University, under David Peakall and others (Cooke 1973, Lincer 1975, Newton 1979, Risebrough 1986). Experimental work also showed that it was only chemicals of the DDT-group that thinned eggshells, but not other organochlorines.

The peregrine is one of the few bird species that breeds on every continent, and has also been studied on every continent. David Peakall and Lloyd Kiff (1988) compiled an influential map, showing the degree of shell-thinning recorded in peregrines across the world, mainly in the 1970s and 1980s. This revealed that: (1) shell-thinning (and hence contamination) was worldwide, even in areas where no DDT was used; (2) some of highest levels of organochlorines and shell-thinning occurred across the arctic, where pesticides were not used, peregrines and prey accumulating these chemicals in wintering areas, and taking them back to the arctic. Not only did this show how transportable DDT/DDE was, it also provided the earliest convincing demonstration of a raptor whose breeding densities and success were determined mainly by events on its wintering areas farther south; (3) low levels of shell-thinning were apparent only in a few areas, such as the Scottish Highlands, where peregrines were resident year-round in areas of no DDT use, and where they were feeding on prey species that were themselves resident in those areas. In these localized areas, peregrines thereby escaped major contamination.

When peregrine populations from different areas were ranked according to their degree of shell-thinning, an interesting pattern emerged (Fig. 5). All those populations with more than 17% shell-thinning declined, while all those with less than 17% shell-thinning maintained their numbers. This comparison revealed the level of shell-thinning in a population (and hence of DDE) that was likely to precipitate population decline.

Some important lessons emerged from this history. First, effects of DDT were insidious, only apparent after several years, and could not have been predicted from testing procedures in operation at the time. Findings showed that pesticides, previously hailed as beneficial to humanity, could have serious environmental consequences. These events led to much more stringent testing of prospective new pesticides. Second, the organochlorines gave us the first well-documented example of a global pollution problem of a kind that we now take for granted with radioactive fallout, greenhouse gases, and other pollutants. Finally, it showed that if a major contaminant was removed, any remaining populations could and did respond by recovery. As an aside, one might mention that the organochlorine crisis kick-started wide-scale research on raptors, and without these pesticides and the problems they created, some might argue that RRF, for example, might never have come into being.

Since the organochlorine era, other problem chemicals have come to the fore. Lead poisoning is of long standing, but is now much better understood as a limiting factor for some raptor populations. The lead comes from lead ammunition, which is obtained by scavenging birds from the unrecovered carcasses of game animals or "varmints" or from the discarded gut piles of shot deer. Poisoning from lead ammunition has emerged as the major factor now limiting the numbers of California Condors (*Gymnogyps californianus*), making it impossible for this reintroduced species to persist in the wild without continual reinforcement of the wild stock from captive-bred birds. Lead poisoning is also killing eagles in North America and eagles and vultures in Europe, but not necessarily enough to affect population levels (Watson et al. 2009).

However, this is the subject of later talks in this meeting, so I will move on to another, more recent, chemical problem, namely the role of the veterinary drug diclofenac in the collapse of Asian vulture populations. Again you all know the story. Within less than ten years, the formerly huge populations of vultures in the Indian subcontinent—estimated to number tens and possibly hundreds of millions—crashed by more than 99%. Various factors were suggested as the cause: a new disease perhaps? But it was the late Lindsay Oaks working for the Peregrine Fund who eventually diagnosed the cause as the non-steroidal anti-inflammatory drug diclofenac widely used on livestock at the time (Oaks et al. 2004). This drug may have killed outright far more raptors than DDT, whose main effect was sublethal. A demographic model showed that if only 0.13–0.75% of carcasses were contaminated by diclofenac in vulture foraging areas in India, populations would be extirpated within a few years (Green et al. 2004). Vultures emerged as especially vulnerable to this drug, which produced characteristic symptoms of uric acid crystals deposited around the gut. With this knowledge, governments in southern Asia acted commendably quickly and banned the veterinary use of diclofenac. However, although the decline in vultures may have halted, the problem is by no means over: first, because there is still some illicit use of diclofenac, which remains available for use on humans. Secondly, other similar chemicals introduced as replacements for diclofenac (such as aceclofenac and ketoprofen) are now also killing vultures, and thirdly, some other scavenging raptors have recently been found dead with the same

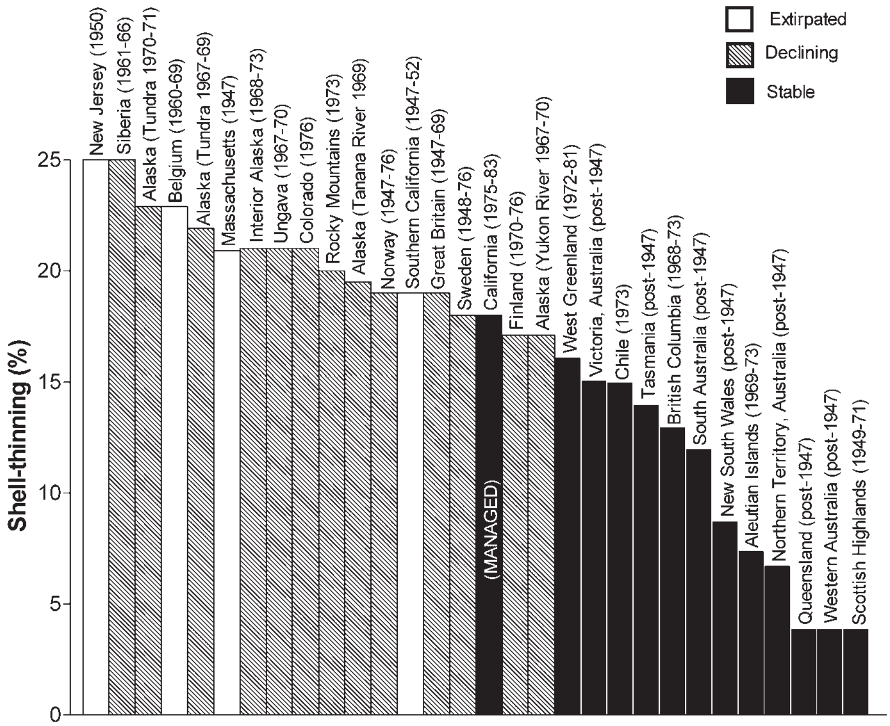

Figure 5. Shell-thinning and population trend in Peregrine Falcons (*Falco peregrinus*) in different parts of the world. All populations showing more than 17% shell-thinning (associated with a mean level of 15–20 ppm DDE in fresh egg content) declined, some to the point of extinction. In the one exception, extra eggs and young were added by biologists to maintain numbers. From Peakall and Kiff 1988.

symptoms as vultures or with drug residues in their bodies, so these drugs are killing more than just vultures. Fourthly, diclofenac and similar drugs have been introduced for veterinary use in other parts of the world, including Spain, where 95% of Europe's vultures now occur (Margalida et al. 2014). There is one positive development though, namely that captive populations of three endangered Asian vultures have now been established in India and, under guidance from Jemima Parry-Jones, all three species are reproducing in captivity, and plans are now afoot for releases in carefully chosen areas.

Captive Breeding. Another important development from the organochlorine era was the captive breeding of peregrines and other raptors for subsequent release. Many people were involved, both here in North America and in Europe; but the undisputed leader was, and still is, Tom Cade. Birds needed be produced and released to the wild on an industrial scale. Captive breeding can, I think, be fairly said to have saved at least two raptors from extinction, namely the Mauritius Kestrel (*Falco punctatus*) and the California Condor, while the peregrine has almost certainly recovered in numbers and distribution in North America much more rapidly than it could otherwise have done. It is hard to believe now that captive breeding met with vigorous opposition at the time, especially for condors, but it has now become a standard method widely used in conservation biology, and not just for raptors.

BIRD MOVEMENTS

The development of radio-tracking in the 1960s gave us for the first time a way of following individual birds around their home ranges, revealing aspects of their behavior otherwise hard to study. It gave us maps showing the home ranges of neighboring birds in the same stretch of habitat, revealing the extent to which home ranges were mutually exclusive or overlapping. Some pioneers, such as Bill Cochran and Grainger Hunt, even put radio tags on migratory peregrines and other raptors and followed them in airplanes (Cochran 1975). Grainger and colleagues followed Bald Eagles from California to Canada (Hunt et al. 1992), confirming a northward post-breeding migration described years earlier by Charles Broley (1947) on the strength of band recoveries from Florida birds. The radio-tagged birds were hard to follow, especially when they crossed national boundaries, but this early work did tell us about the migration speeds of some raptors and where and when they stopped.

A much bigger advance came with the development of satellite-based radio-tracking through which individual birds could be followed through their entire migrations, wherever on earth they flew, and wherever they wintered. One of the earliest maps showing a complete migration was compiled by

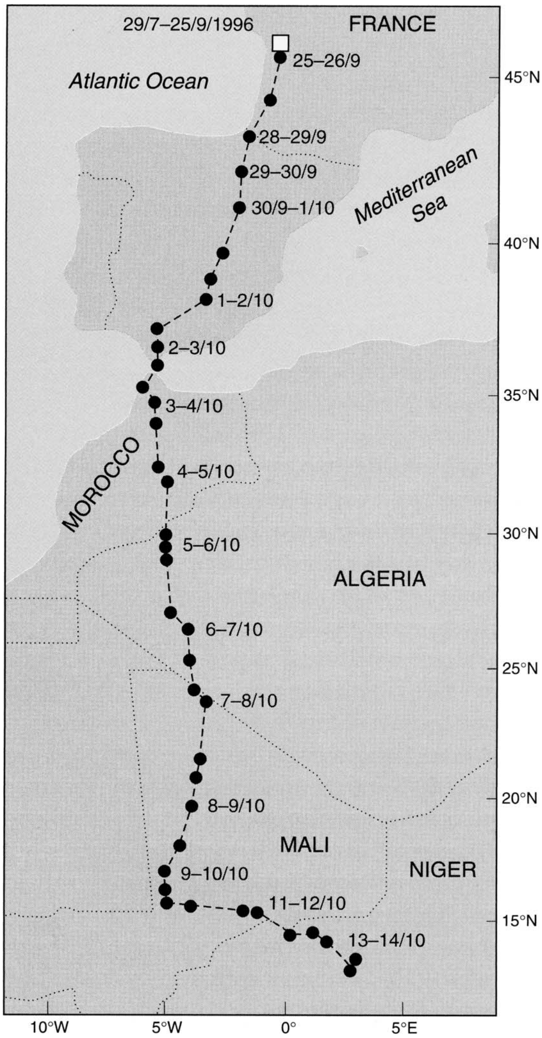

Figure 6. Migration of a satellite tracked radio-tagged Short-toed Eagle (*Circaetus gallicus*) from France to Niger, showing the daily distances and the nightly stopping places. Adapted from Meyburg et al. 1998, with permission from *Alauda* journal.

Bernd Meyburg and colleagues (Meyburg et al. 1998). This map dates from the 1990s and shows the journey of a single Short-toed Eagle (*Circaetus gallicus*) tagged at its nest in France, and followed to its wintering area in Niger in West Africa (Fig. 7). The spots mark where this bird roosted each night. This was clearly an enormous advance on bird banding: it revealed the precise route the bird took and the duration of its journey. It showed where the bird spent each night, and how far it travelled each day. You could look up the locations on Google Earth and see in what sort of habitat the bird spent each night, and from the route you could see in what ways, if at all, the bird had been affected by weather.

Some biologists were able to tag and follow many individuals of the same species from different parts of the range. Work by Mark Fuller and colleagues on Swainson's Hawks (*Buteo swainsoni*) confirmed the route from prairies to pampas and particularly the bottleneck through Panama and the narrow route through South America to the grasslands of Argentina; and for peregrines the same group confirmed a more broad-front migration involving longer sea-crossings, but largely different routes in fall and spring, with many individuals travelling southward down the east coast in fall, and northward up through the center in spring (Fuller et al. 1998). Satellite tagging thus opened the doors on a new wonderland, resolving previously unanswerable questions on bird migration: the precise routes taken, the duration of the journey, the stopping places, and so on. The method improved and expanded, being applied to many species in many parts of the world, so that the resulting data are now commonplace.

Satellite tracking also revealed for some species previously unknown wintering areas, or previously unknown behavior, as illustrated by some work by Kurt Burnham on Gyrfalcons (*Falco rusticolus*; Burnham et al. 2011). Some birds tagged in northwest Greenland spent their winters at sea: they became seabirds, seldom coming to land. These birds were presumably resting on icebergs, hunting seabirds, behavior previously unknown, at least on this scale. They ranged over huge areas in winter, so that their ranges during October–March spanned an average of 160,000 km^2. However, the falcons moved south during winter, as advancing ice pushed their prey southwards. Adults returned to their breeding areas early, before other birds, when the sea ice was at its maximum extent and when the only prey available in breeding areas was the Rock Ptarmigan (*Lagopus muta*). Other prey arrived later. This dependence on ptarmigan for several weeks in spring explains why the breeding of Gyrfalcons fluctuates so closely in accordance with ptarmigan numbers; it is all the falcons have to eat in some areas for the first third of the breeding cycle. This study provided an example of how technology is changing our idea of what birds do, and where they spend the winter. Other radio-tagging work has given examples of satellite-tagged birds migrating to previously unknown wintering areas, thereby extending our knowledge of the geographical range.

CONCLUSIONS

So what has been achieved in the past 50 yr? In the 1960s we knew relatively little about raptors. In Europe and North America, they were some of the least known of all birds. Academics had tended to avoid them because they were difficult to study. My own Ph.D. supervisor, David Lack, advised me against working on raptors. They were too thin on the ground, he said, and far too difficult to study; I would never get samples big enough for worthwhile analysis. On this occasion, though, eminent as he was, I ignored his advice. There were, however, some pioneers among biologists who had already laid foundations for the rest of us by their efforts in the field: in North America there were the Craighead brothers (authors of Hawks, Owls and Wildlife), Joe Hickey with his early study of peregrines, Frances Hamerstrom with her study of harriers (*Circus cyaneus*); in Europe we had Derek Ratcliffe on peregrines, Leslie Brown and others on Golden Eagles, and Yngvar Hagen in Norway on arctic-nesting raptors and lemmings. But these early pioneers could be counted on two hands.

As a result of community effort, we now know a lot more about the general biology of raptors, about the factors that limit their numbers and breeding success, about various human impacts, and about their migrations and behavior. We also have regular survey and monitoring systems in place, including the many migration watch sites, building on the pioneering work at Hawk Mountain. We have excellent field guides by Bill Clark and others, and we have handbooks of methodology. We have learnt to breed raptors in captivity, and reestablish viable populations in the wild. The California Condor and Mauritius Kestrel were saved from extinction; the peregrine is perhaps more numerous now than at any time in the historic past. And we have a strong and active community of young raptor researchers taking us into the future. All this is the result of a strong collaborative community effort, in which the RRF—with its journal and its meetings—has been at the center now for half a century. We seem well set for the future, because the one thing we can count on is that more unforeseen threats to raptor and other bird populations will emerge in the years ahead.

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