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Linking Raptor Migration Science to mainstream Ecology and Conservation: an ambitious agenda for the 21st Century

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ABSTRACT

Raptor-migration specialists know much about the seasonal movements of the birds they study. The status of the field is especially solid with regard to spatial and temporal patterns of migration. We know considerably less about causes and consequences. To date, progress in the field has been methodical, incremental and predictable; with most efforts focusing on the natural history of the raptors themselves, and with workers in the field talking more to each other than to potential colleagues in other areas of ecology and conservation. I maintain that the greatest advances yet to come will accrue to those who (1) form partnerships and integrate their efforts into the larger fields of bird-migration studies, mainstream ecological research and conservation biology, (2) operate at scales appropriate for the questions at hand and (3) take advantage of emerging technologies and resources. A series of initiatives is offered, intended to supplement and broaden existing efforts. These include investigating (1) the extent to which raptors engage in broad, frontal rather than narrow, corridor migration, (2) how spring and autumn migration strategies differ and why, (3) the proximate and ultimate causes of partial migration, (4) how raptors circumvent barriers to migration behaviourally and physiologically, and (5) how human-induced habitat changes and global-climate change may be affecting raptor migration. I also suggest expanding the use of geographic information systems (GIS), satellite telemetry and networks of observers in multi-site, large-scale studies of migration ecology and conservation.

INTRODUCTION

Long-distance raptor migration represents the most spectacular movement of land-based predators on earth (Bildstein *et al.* 1995). Migrating raptors have fascinated humanity for millennia, from the Old Testament (Job 39: 26-29 to published New World accounts dating from within 30 years of European settlement (Baughman 1947). Today, premier watchsites, such as Eilat in Israel and Hawk Mountain Sanctuary in the United States (Allen *et al.* 1995), attract tens of thousands of visitors annually. In North America, The Hawk Migration Association of North America - with more than 800 members - is devoted entirely to the study and conservation of migrating raptors.

As a result of this long-standing interest, raptor-migration specialists possess an enviable record of many aspects of raptor migration (*cf.* Kerlinger 1989). Indeed, with the possible exceptions of waterfowl and shorebirds, the migratory patterns of the world's 133 species of irruptive, partial and complete raptor migrants (*sensu* Kerlinger 1989) are better documented than those of any avian taxon. Studies of migrating raptors have made major contributions to conservation biology.

Individuals interested in a recent and thorough summary of raptor-migration science should consult Kerlinger 1989, and references therein. My focus is on the future of the field: what remains to be done - and more importantly - how we might go about doing it.

My arguments are based on two assumptions: (1) Although we know much about the fundamental features of raptor migration, we know relatively little of its causes and consequences. (2) The reason for this is because many workers in the field are raptor specialists (i.e. individuals with relatively narrow species and taxonomic affinities), rather than general ecologists or conservation biologists (i.e. individuals with broader evolutionary, physiological, ecological or conservation orientations).

I believe that major advancements in our field will most likely accrue to those who (1) form new partnerships and integrate their efforts into the broader fields of bird-migration study, mainstream ecology and conservation biology, (2) operate at the appropriate spatial and temporal scale for the questions at hand, and (3) take advantage of emerging technologies and resources.

Below, I provide a brief rationale for expanding our efforts in these areas, and then outline an agenda for doing so. Because I believe that students of raptor migration have not been communicating with potential colleagues in other subdisciplines as much as they might, I specifically emphasize references outside the field of raptor migration.

THE RATIONALE FOR BROADENING THE SCOPE OF OUR EFFORTS.

To date, progress in raptor-migration science has been methodical, incremental and, for the most part, predictable. Most effort has focused inwardly on the natural history of the raptors themselves, rather than on more broadly theoretical and ecological aspects.

Overall, very few studies have formulated hypotheses, stated and tested predictions and revised existing hypotheses in the light of more recent results (but see Kerlinger 1989). In the next century, students of raptor migration will need a wider range of skills than those of their predecessors. We will need to communicate more freely and integrate our efforts with those of other scientists and conservationists, and adopt new approaches if we wish to continue to make progress in our field.

Integrating our efforts with those of others outside our field.

The history of ecology is filled with examples of the critical role that cross-discipline integration has played in advancing scientific progress (Cohen 1985; Jones & Lawton 1995). Unfortunately, the very breadth of the discipline generates specialisation and fractionisation. Much of the information generated by specialists in various fields of ecology goes largely unnoticed by workers in others (Root 1987). All of us know what "we" are talking about, but few outside our subdisciplines do. We need to communicate more frequently with those outside our immediate areas of expertise.

If we are to accept this challenge, raptor-migration specialists will need to seek out the new thoughts and innovative technologies colleagues in other subdisciplines have to offer. One especially appropriate place to start would be the broader field of avian migration science. Three contemporary monographs on bird migration, Alerstam (1990; Swedish edition 1982), Gwinner (1990), and Berthold (1993; German edition 1990) provide accessible up-to-date summaries of recent progress in the field. All three references include a wealth of comparative information on what is - and more importantly - what is not known in the field. In addition, all three place raptor migration within the broader context of the avian migration literature (Table 1). Alerstam (1990), especially, draws heavily upon the raptor-migration literature for major portions of his presentation. In an age where it is increasingly difficult to keep pace with the published literature, these three references provide ready access to new thoughts and innovations in the broader field of avian migration science. Together with Kerlinger (1989) they should be read by anyone contemplating research on migrating raptors.

Conservation biology - the study and protection of biodiversity - is another field in which we should seek new partnerships. One of the greatest challenges faced by conservation biologists is to link their integrative science

Table 1. Numbers of diurnal raptor species mentioned, and pages devoted all or in part to raptor migration in three contemporary monographs with the title "Bird Migration".

Monograph[a]	Number of raptor species mentioned	Number of pages on which raptors are mentioned (% of text pages)
Alerstam (1990)	52	72 (18%)
Berthold (1993)	15	12 (6%)
Gwinner (1990)	14	15 (4%)

[a]Complete citations are provided in the references section.

to that of subdisciplines in the field in ways that produce simple and effective conservation messages for land managers and decision makers (Allen & Hoekstra 1992). General introductions to this rapidly developing field can be found in Primack (1993) and Meffe and Carroll (1994). An especially useful summary as it applies to birds appeared as a recent supplement to the *Ibis* (Coulson & Crockford 1995).

Working at the appropriate scale.

For logistic and other reasons, ecological research frequently focuses on single species or species groups, usually within small spatial and brief temporal scales (Tilman 1989; May 1994). Ecological patterns and processes, however, occur across numerous spatial and temporal scales. Working at a scale appropriate for the question at hand is the key to gaining insights into ecological process (Wiens 1989). The "appropriate" scale depends upon both the species being investigated and the questions being asked. Edwards *et al.* (1994) provides an excellent introduction to the importance of scale in ecology and conservation.

Ecological phenomena frequently operate at scales that prohibit the use of short-term, small-scale investigations. In many instances, long-term substantial investments are needed to understand how single species and entire systems function within their ecological domains. This is especially true in conservation biology, where an ability to predict ecological events requires an understanding of the temporal and spatial scales over which populations normally fluctuate. For example, much of the current debate regarding reasons for declines in populations of many neotropical migrant songbirds results from our ignorance regarding the habitat needs of these species throughout their wide ranges (*cf.* Terborgh 1989).

Many species of migratory raptors inhabit enormous "ecological neighbourhoods" (*sensu* Addicott *et al.* 1987). Studies of these species need to be conducted at the appropriate scale. Unfortunately, researchers working at different sites along important migratory corridors and at different ecological scales frequently fail to communicate the results of their efforts to one another (Bildstein *et al.* 1995; Malmer & Enckell 1994). We need to link such efforts more fully than we have in the past.

Taking advantage of new technologies and resources.

Raptor-migration science has changed considerably since the turn of the century. New technologies and even new disciplines have emerged. Radio-transmitters, computers, geographic information and global position systems, and other sophisticated pieces of equipment have been added to a field arsenal that used to consist of binoculars and note pads. These new tools offer ample opportunities for those willing to learn how to use them. What follows is a synopsis of several of the more significant advancements in this area.

Landscape, or geo-ecology as it is sometimes called, is a relatively new, systems-orientated, synthetic approach to spatial environmental interactions. Initially designed to determine how spatial considerations affect the way humans interact with their environments, the field has grown to include studies of other spatially explicit environmental interactions as well (Zonneveld 1990; Naveh & Lieberman 1994). Currently, the field is focusing on how habitat mosaics and the spatial patterns of ecosystems affect ecological features and functions (Wiens 1992). Successfully employed, landscape ecology provides a landscape-scale view of organism-environment interactions that complements, in our case, a bird's-eye view of such interactions. This field is proving to be especially useful in studies of habitat fragmentation and biodiversity.

Remote sensing involves the use of technology to acquire information from a distance by physically unattached means. A thorough review of this technology and its applications in landscape ecology can be found in Naveh and Lieberman (1994). A more specific example is provided by Green and Sussman's (1990) assessment of deforestation rates in Madagascar.

One of the earliest uses of remote sensing technology in the field of raptor migration ecology involved the use of *radio telemetry* in the early 1960s (e.g., Southern 1964). Today, advances in the field include substantial miniaturisation of radio transmitters for use on smaller raptors (Kenward 1987), and the use of satellite receivers for tracking long-distance movements of larger raptors (e.g., Meyburg *et al.* 1993; Meyburg & Lobkov 1994). The latter, especially, has tremendous potential for use in migration studies.

Another facet of remote sensing that remains largely unused involves *aerial and satellite photography* (Naveh & Lieberman 1994). Coupled to landscape ecology, and used in conjunction with even modest geographical information systems (GIS; Shaw & Atkinson 1990), this aspect of remote sensing is already producing large-scale ecological maps with enormous amounts of spatially-explicit data of considerable value to raptor migration ecologists.

A recently digitized map of the extent of human-induced fragmentation and flow regulation of 139 of the largest North American, European and former Soviet Union river systems (Dynesius & Nilsson 1994) is just one example of the databases available for migration-map overlays. Another is a recently-mapped global inventory of the extent of human disturbance across Udvardy's (1975) widely used biogeographic classification scheme (Hannah *et al.* 1994). The latter, designed specifically for use by field conservationists, is fully executable on a personal computer with 286 processing, and as little as 40 megabytes of hard-drive memory (Hannah *et al.* 1994). Both offer considerable potential for integration with existing raptor-migration databases.

An emerging interest in **the use of biotic corridors in conservation** (Hudson 1991; Spellerberg 1991) has resulted in the establishment of a number of locally-based human networks (Saunders *et al.* 1995) working together to achieve common goals. Networks provide a human-resource base with which individuals studying the large-scale movements of long-distance raptor migrants can share information and resources. *Hawks Aloft Worldwide*, Hawk Mountain Sanctuary's global conservation initiative for migratory raptors, is an example of this type of cooperative effort (Bildstein *et al.* 1995).

International wildlife law offers considerable opportunities in this area as well. Consider, for example, the Convention on the Conservation of Migratory Species of Wild Animals (CMS)(Lyster 1985). First proposed at the 1972 United Nations Conference on the Human Environment, CMS, or the Bonn Convention as it is sometimes called, came into force in November 1983, and offers a framework for conserving migratory species and their habitats. As of early 1994, CMS comprised 43 parties from throughout the world. Parties are encouraged to offer agreements providing for specific initiatives for populations of species that regularly cross international boundaries. Agreements for migratory bats in Europe, Siberian Cranes *Grus leucogeranus* in western and central Asia, and cetaceans in the Baltic and North seas were in place in early 1994. Agreements for Houbara Bustards *Chlamydotis undulata* and Slender-billed Curlews *Numenius tenuirostris* were under consideration at that time (Goriup 1994). The Bonn Convention appears to provide a potentially effective mechanism for the international conservation of raptors along important migration corridors as well.

AN AGENDA FOR THE FUTURE

1. Body size and migratory behaviour

Given the general relationship between increased body size and an ability to survive under more variable or extreme climatic conditions (Boyce

1979), we might predict that outside the tropics, within closely related groups, larger species would be less migratory than smaller species. Do raptors exhibit this pattern, and if not, why not?

2. Partial migration and the control of migration tendencies.

Flexibility in migration behaviour in the face of environmental change may be critical to the survival of certain raptors (Dolman & Sutherland 1994). The fact that most migratory species are partial rather than complete migrants (i.e. some, but not all individuals migrate; Kerlinger 1989), suggests considerable variation in migratory tendencies within species. A number of extrinsic and intrinsic factors, including weather, autumnal aggressive behaviour, social status and date of hatching are known to influence migratory behaviour in partial migrants (Berthold 1984; Schwabl & Silverin 1990). With few exceptions (Mueller *et al.* 1977), the extent to which these and other factors affect the migratory tendencies of raptors remains unknown. Investigations of hormonal control of partial migration are also lacking, as are studies of the extent to which migratory tendencies are culturally and genetically controlled in individuals (cf. Berthold 1993; Dolman & Sutherland 1994).

Studies of nonraptors suggest that birds modify their migratory habits when conditions merit it (Dorst 1962; Berthold 1993; Dolman & Sutherland 1994). The degree to which widespread human-induced reductions in biodiversity, habitat modification and global climate change, together with recent shifts in the intensity of human predation, may influence the migratory tendencies of raptors remains largely unexplored, (see Dolman & Sutherland 1994 for a theoretical approach to this question). The few studies that do exist (Juillard 1977; Sodhi *et al.* 1992; Gatter 1992) suggest that substantial changes may occur. Recent work at Hawk Mountain Sanctuary, for example, suggests that during the 1980s a period of relatively mild winters in eastern North America may have resulted in Sharp-shinned Hawks *Accipiter striatus* remaining farther north than they did earlier in the century (Viverette *et al.* 1996) (Table 2). Whether this is occurring in other species remains unknown.

3. Geographic barriers to raptor migration

The major oceans, mountain ranges and deserts of the world present potentially formidable barriers to migration. Although migrating birds of prey seldom cross large bodies of water, many regularly fly over mountains and deserts (Kerlinger 1989). Oxygen availability during mountain crossings, water loss during desert crossings, and temperature stress during both have received little more than theoretical attention to date. Although many migratory raptors are known to adjust their orientations to account for local and regional topographic, climatic and ecological features, little is known of the costs and benefits of these decisions.

Consider, for example, the potential impact of physiological obstacles presented by the triple Palaearctic barrier (*sensu* Berthold 1993) of the Alps, Mediterranean Sea and Sahara Desert. How do trans-barrier migrants cope with these hurdles, and what are the fitness and life-history consequences? Most major Nearctic mountain chains are aligned north-south, while most Palaearctic mountain chains run east-west. To what extent are these differences correlated with the migratory tendencies and behaviour of raptors in the two regions? A comparative investigation of the flight anatomy and migratory tendencies of European, Asian and North American populations of circumboreal long-distance migrants (or comparative studies of migratory ecological counterparts in the three regions) would be a useful guide.

4. Physiological consequences of high-altitude flight

The oxygen-delivery system , or haemoglobin physiology, of migrating

Table 2. Species of raptors whose migratory behaviour has changed recently.

Species	*Circumstance (reference)*
Red Kite (*Milvus milvus*)	recently expanded their overwintering areas northward in Switzerland in response to an increase in garbage dumps (Juillard 1977)
Bald Eagle (*Haliaeetus leucocephalus*)	throughout much of North America the migratory tendencies of this species appear to be influenced by local resource availability (McClelland *et al.* 1994; Bryan *et al.* in press)
Sharp-shinned Hawk (*Accipiter striatus*)	Sharp-shinned Hawks in eastern North America appear to be expanding overwintering areas northward, possibly in response to increased prey availability (Viverette *et al.*, 1996)
Broad-winged Hawk (*Buteo platypterus*)	in eastern North America this species' migratory habits may have undergone several recent changes, with south-bound birds possibly following more easterly routes to take advantage of heat-island effects of major metropolitan areas (Goodrich 1986), and indivudals wintering farther north (Brown & Amadon 1968).
Swainson's Hawk (*Buteo swainsoni*)	migratory short-stopping of small populations of this normally transcontinental migrant appears to be occurring in both the eastern (Browning 1974) and western (Yee *et al.* 1991) United States.
Merlin (*Falco columbarius*)	in the Canadian Great Plains Merlins have expanded their overwintering areas northward in response to increased prey availability in large cities (Kerlinger 1989).

raptors remains largely unstudied. Haemoglobin polymorphisms provide a system in which altitude-specific forms of the oxygen-carrying molecule exist side-by-side in the circulatory system, thereby ensuring a sufficient supply of oxygen at a variety of altitudes (Berthold 1993). Recent investigations of Rüppell's Griffon *Gyps rueppellii* indicate that this especially high-flying partial migrant produces four distinct forms of haemoglobin, rather than the two found in most avian migrants (Hiebl & Brainitzer 1988). The extent to which this and other physiological adaptations (e.g. shifts in haematocrit and haemoglobin concentrations with altitude, etc.) occur in other migrating raptors is unknown. Additional investigations on both inactive and flying birds appear warranted.

5. Water balance on migration

Several species of raptors have been reported to engage in hyperphagia and excessive fat deposition prior to migration (Glutz von Blotzheim *et al.* 1971; Gessaman 1979; Geller & Temple 1983), and it is widely held that fat plays a major role as an energy source for migratory birds of prey (Kerlinger 1989). Although fat is by far the most energy-dense fuel resource available to migrating birds, its use is not without cost. Energy is not the only concern. Water budgets, especially during desert crossings, also may be critical (Yapp 1962). Fat is normally stored dry, presumably to lighten the bird's aerodynamic load (Berthold 1993). But fat delivers relatively little metabolic water during catabolism (i.e. 26.3 mg of water Kj^{1} fat oxidized), and the question of how soaring migrants deal with the potential water shortfall remains unclear. Studies of Australian and trans-Saharan migrants (Skadhauge 1974; Haas & Beck 1979) suggest that high-speed, continually flapping passerines have developed effective strategies for water conservation while flying over deserts (Biebach 1990). Whether raptors have done the same is unknown. Considerable contributions in this area of research remain to be made.

6. Moult and migration behaviour

Is there a typical moult pattern for migrating raptors, and if so, what is it? How does it compare with those of other avian migrants? If there is no general moult pattern, are interspecific differences associated with certain extrinsic (i.e. geographic) or intrinsic (i.e. anatomical, taxonomic, gender or age class) parameters?

How, for example, do raptors deal with the potentially competitive energetic demands of simultaneous moult and migration, or, for that matter, of premigratory moult and fat deposition (cf. Lindstrom *et al.* 1994)? Do raptors suspend or slow moult during migration, and if not why not? Do any species interrupt their migratory journeys to moult (i.e. undertake a modified non-flightless form of moult migration that occurs in many waterfowl and several other kinds of birds; e.g. Salomonsen 1968; Jehl 1990). Do species undergoing premigratory fat deposition also engage in premigratory moult? Kjellén's (1992) recent report of moult being slowed or interrupted in raptors migrating though Falsterbo, Sweden, and hastened thereafter, provides an example of this type of study.

7. Soaring and migration

Despite considerable attention in the literature, much remains to be learned about the role of soaring (Kerlinger 1989). To what extent do raptors depend on soaring to complete their migrations? Do raptors that engage in soaring do so both on fall and spring migration? If so, how, and if not, why not?

8. Flocking on migration

Flocking is a trademark behaviour of several species of holarctic migrants. The extent to which this is linked to diet and length of migration is relatively well known (Kerlinger 1989). However, how flocking in turn affects migration strategies is largely unstudied. For example, Leshem (1994) reports that flocking species pass through Eilat, Israel, over shorter time periods than do non-flocking species. The same appears to be true at Hawk Mountain Sanctuary. At the latter site, the relatively early passage of Broad-winged Hawks *Buteo platypterus*, a flocking species, may be linked to this species' attempt to move through the region in early autumn, a time when thermals conductive to soaring flight remain a somewhat predictable resource. Whether this holds for other species in other areas remains unknown.

9. Broad frontal migration

Much of what we know about raptor migration has been obtained from studies at migratory bottlenecks (Kerlinger 1989). Yet many species of birds, including many raptors, move across broad fronts during most of their migratory journeys (Berthold 1993). The degree to which broad-frontal migration occurs, the behaviour of raptors during such movements, and the fitness consequences of doing so are largely unstudied. The use of satellite telemetry offers considerable promise in this area. Specific questions to address include: How frequently do raptors use broad frontal migration? Where and when do they do so, and why? Are raptors more likely to feed during broad frontal migration than when flying along narrow migratory corridors? Is frontal migration species or age specific? What are the relative costs of broad frontal migration versus migration along narrow migratory corridors?

10. Spring versus autumn migration

In many species of birds, individuals migrate faster and are more likely to migrate across broad fronts during spring than during autumn. Some European passerine migrants, for example, take only one third to one half as much time to return to their breeding ground each spring as they do flying in the opposite direction each fall (Berthold *et al.* 1990; Pearson 1990). Standard explanations for more rapid migratory movements in spring than in fall include (1) that although birds are reluctant to leave their breeding grounds while food is still plentiful in fall, they are eager to return to them in spring to breed (Dorst 1962), and (2) that young birds, having learned their migratory routes during autumn migration can return more rapidly to their breeding grounds the following spring (Berthold 1993). Thus, for example, Leshem (1994) has argued that although the overall period of migration for each species migrating past Eilat, Israel, appears to be longer in spring than in autumn , arrival percentages on peak days are higher in spring than in autumn because the adult population is hurrying back to their breeding grounds then.

Clearly additional work is needed in this area, both with regard to determining the extent to which the phenomenon occurs and, if indeed it does occur, the extent to which internal versus external forces are responsible for it. For example, do spring migrants move faster because of internal forces, such as those mentioned above, or because of external forces such as food being more available during autumn migration than in spring, or weather being better in spring than in autumn? A simple test of the latter's applicability would be to compare the relative autumn and spring passage rates of raptors that do and do not feed on migration,

11. Timing of arrival on the breeding grounds

Raptors arriving too early on their breeding grounds may face inclement weather and depressed prey availability. Those arriving too late, however, may not be able to find high quality territories or mates, and even if they do, may not have sufficient time to produce high quality young (e.g. Daan *et al.* 1989). Although arrival times are generally thought to be adaptive, studies linking the timing of spring migration with its fitness consequences are uncommon. Moller's recent investigation of spring arrival time and its consequences in migratory Barn Swallows *Hirundo rustica* (Moller 1994) provides a useful framework for this type of investigation. American *Falco sparverius* and Eurasian *F. tinnunculus* Kestrels, Ospreys *Pandion haliaetus* and other raptors attracted to nest boxes and nesting platforms appear to be ideally suited for similar investigations.

12. Effects of parasitic infestation on migration and vice versa

Recent evidence suggests that internal parasites can interfere with the long-distance migratory behaviour of shorebirds (cf. McNeil *et al.* 1994). The extent to which this also may occur in raptors remains an unexplored topic. Most migratory raptors are partial migrants. Studies comparing the parasitic loads of migratory and nonmigratory individuals in such species could provide insight into the factors affecting these different strategies. Another approach would be to collect information on parasite loads from migrants en route. Questions to be asked include: are infested birds less likely to migrate than those that are not infested? Do late migrants carry heavier parasitic loads than do individuals that pass earlier? Do raptors carry heavier loads at the end of their journeys than when they set out? Many of the same questions also could be asked regarding different pesticide loads.

Conversely, the extent to which long-distance migration, in turn, affects an individuals raptor's levels of parasitic infestation remains unknown (*cf.* Loehle 1995). Consider, for example, the different parasitic regimes faced by migratory and sedentary populations of raptors. Although migratory species may avoid the continual build-up of parasites by moving between seasons, overall they are likely to be exposed to more species of pests than their sedentary kin. Are the parasitic infestations of migrants more episodic than those of sedentary raptors? How does long-distance migration affect the ability of internal parasites to locate appropriate intermediary hosts? Do migrants have greater levels of parasitic diversity than sedentary species?

13. Annual variability in migration passage rates

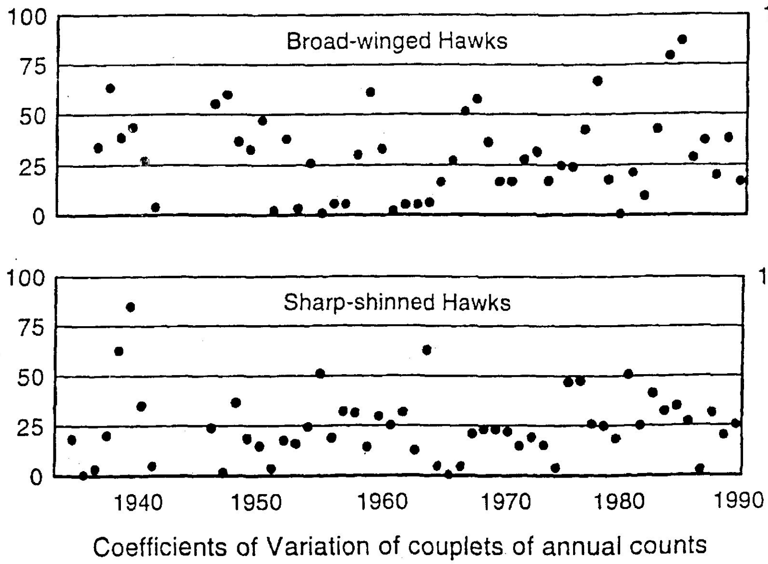
Many hawk migration watch-sites have amassed long-term (i.e., >10 years) data sets regarding annual passage rates of raptors (e.g., Bednarz *et al.* 1990). To date, most analyses of these have focused on long-term changes in mean values over time rather than on short-term, interannual fluctuations. Indeed, in most instances the former are regarded as the biological signal of note, while the latter are considered to be noise. However, recent evidence suggests that short-term variation also may be an important part of the signal, with increases in short-term variation being linked to increases in human perturbation (Karr *et al.* 1987). Analyses of existing databases for shifts in short-term variation such as the example provided in Figure 1 are long overdue.

14. Migrating raptors as bioindicators

Almost half a century ago, declines in annual counts of several species of migrating raptors at traditional watchsites in eastern North America were used to confirm the widespread infiltration of DDT into the aquatic ecosystems of that continent (Carson 1962; Hickey 1969). Population shifts, however, typically represent complicated and frequently indirect relationships between birds and environmental change (Temple & Wiens 1989). Behavioural and physiological responses to environmental change are usually both more direct and immediate. Long-term studies of changes in the behaviour and physiology of migrants offer considerable potential for the use of migrating raptors as

Figure 1.

Long-term variation in between-year variability in the annual counts of Sharp-shinned Hawks *Accipiter striatus* and Broad-winged Hawks *Buteo platypterus* at Hawk Mountain Sanctuary, 1934-1991 (a), compared with long-term variation in numbers of birds seen annually (b). Between-year variability expressed as Coefficients of Variation (CV) of couplets of annual counts for consecutive two-year periods between 1934 and 1942, and 1946 and 1991 (No counts were conducted from 1943 through 1945 at the site. The CV [i.e., the standard deviation x 100/the mean] is an independent unit of measurement expressed as a percentage of the mean. CVs are directly comparable across species. Note the lack of any long-term trends in between-year variability in these two species despite considerable long-term variation in overall population numbers).



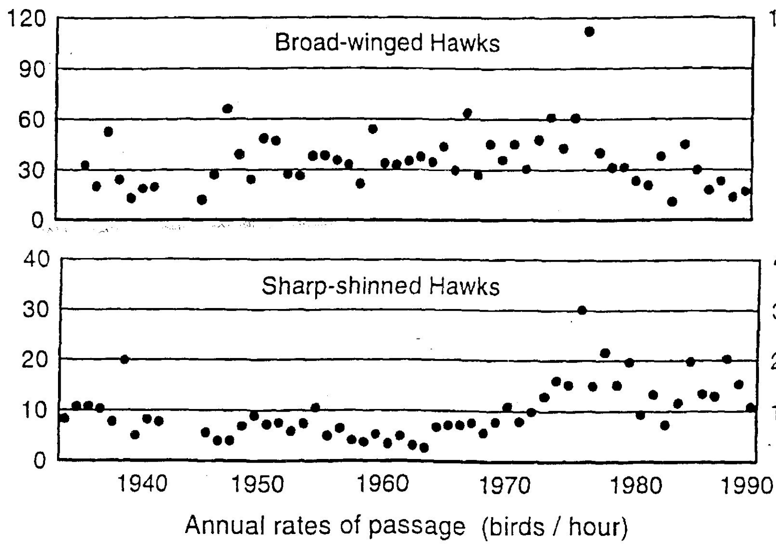
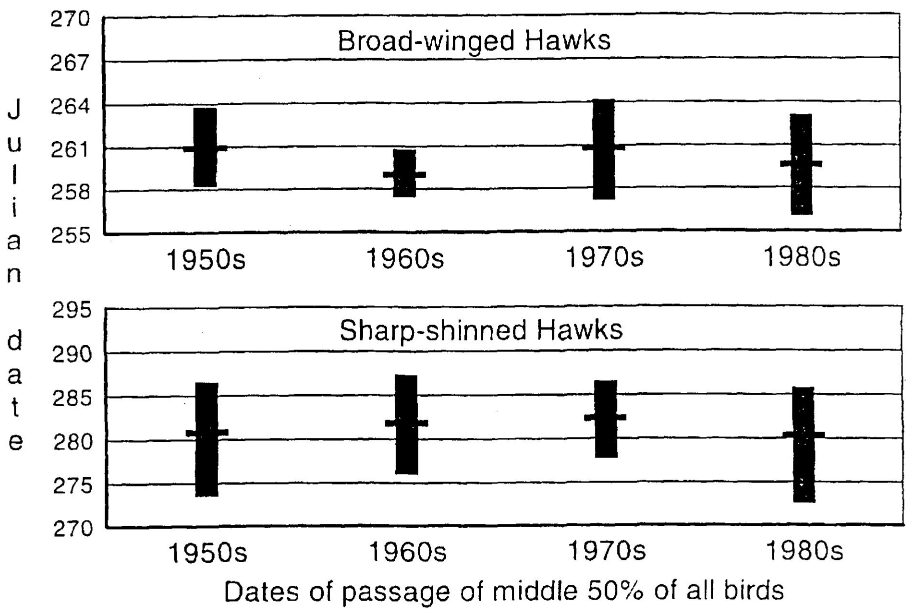


Figure 2.

Long-term variation in migration phenology of Sharp-shinned Hawks *Accipiter striatus* and Broad-winged Hawks *Buteo platypterus* at Hawk Mountain Sanctuary, 1950-1990. Horizontal lines indicate the mean Julian date by which 50% of all birds have been seen in each decade. Vertical bars indicate the mean period over which the middle 50% of all birds are seen each decade. Although the mean date of 50% passage did not differ among decades for either species (P>0.05; Analysis of variance with Duncan' multiple ranges tests), the period of time over which the middle 50 % of the flight occurred was significantly shorter in the 1960s than in either the 1970s or 1980s for Broad-winged Hawks and significantly shorter in the 1970s than in either the 1950s or 1980s for Sharp-shinned Hawks (P<0.05; Analysis of variance with Duncan' multiple ranges tests).



truly "leading-edge" indicators of environmental change. Changes in timing of migration, for example, could be used to indicate shifts in breeding phenology, or in the breeding range of species. Changes in fat content, blood-parasite loads, or water metabolism, might be indicative of shifts in environmental stress.

15. Source populations

Recent advances in molecular genetics have revolutionized our abilities to determine the genetic composition of migrating raptors. Determinations of the genetic profiles of migrants at individual watchsites, coupled with concurrent studies of the same species on their breeding and wintering grounds, could provide important insight into the migratory routes and year-long habitat needs of specific raptor populations and, in turn, their vulnerability to human interference.

16. Satellite telemetry

Conventional, land-based telemetry has limited applicability for tracking long-distance movements (cf. Jouventin & Weimerskirch 1990). The recently developed technology of satellite telemetry offers considerable promise for raptor migration research. Indeed, initial studies (e.g., Meyburg *et al.* 1993; Meyburg & Lobkov 1994) involving raptors strongly suggest this technology will be useful in addressing a number of issues, including: how far, fast, and with how much daily variability do long-distance migrants move over short periods of time? Do individuals of the same species employ different movement strategies on migration and, if so, what are the fitness consequences of such differences? Do individuals employ different strategies among years, and if so, why?

CONCLUSIONS

Three forces drive the rate at which scientific knowledge progresses. The first is serendipity. The second is advancing technology and the new instrumentation it produces. The third is the appearance and acceptance of new paradigms that help shape the kinds of questions we ask (Malmer & Enckell 1994). Raptor-migration specialists have embraced the first two much more than the latter. The theories and scientific methods we employ today are far more similar to those of 50 years ago than the technology with which we pursue our efforts.

The 21st century is not far in the future and, in fact, much of the research we undertake today will not become part of the literature until then. As our science enters the new millennium, I challenge my colleagues in raptor-migration science to be innovative, to test new and different hypotheses, to form new partnerships and interact with scientists in other disciplines, to integrate their data with existing spatial data sets, to work at the appropriate scale for the questions at hand, and to share their information with new audiences; in sum, to take risks and expand the scope of their research and conservation efforts. Doing so promises many rewards.

Finally, an important caveat is in order: Many of our current efforts continue to provide important new insights into the whys and wherefores of raptor migration, as well as significant information on the status of current raptor populations and the ecosystems they inhabit. The new initiatives suggested above are intended to broaden and strengthen these efforts, not to replace them.

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