MANAGEMENT OF PREY HABITATS AND POPULATIONS

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Abstract: Raptors depend upon their prey in the same way that all consumers depend upon their food resources, yet the tie appears stronger in most raptors because of the specialization of their diets. Most raptor populations show changes in reproductive rates, both in effort and in success, associated with changes in prey populations. Many raptor populations fluctuate in concert with their prey populations. Mass emigrations from boreal regions are correlated with prey population collapses in those regions. Taken together, these observations suggest that under many conditions raptors are limited by their prey populations. Is there potential to increase raptor populations by managing their prey habitats and populations? We will answer this question by discussing a series of questions: (1) Can we increase prey through habitat manipulations? 2) Can we increase prey through direct population manipulations? 3) If we increase their prey, will raptor populations increase? Managing prey populations is one of the least explored approaches to raptor management. Though fraught with difficulty, it offers enormous potential. Occupying the highest levels of the ecological pyramid in most communities, raptors are sensitive to changes at almost any level in these communities, but especially at the levels of their prey, the primary and secondary consumers. Management activities occurring in these communities may impact raptors directly or indirectly through changes in prey populations and habitats. In this paper, we will examine the evidence for the close relationship between raptors and their prey and then evaluate the potential for managing raptors through their prey habitats and populations.

RAPTOR DEPENDENCE ON PREY POPULATIONS

Evidence for the dependence of raptors upon their prey populations requires simultaneous study of both the raptors and their prey over several years. Such studies are obviously difficult to conduct, yet they provide significant insight into the interrelationships between these dynamic populations. Such studies have documented changes in raptor reproductive rates, both in effort and in success, associated with changes in prey populations. Mass emigrations from regions have been associated with prey population collapses in those regions. Perhaps most significant are the many studies which show raptor populations fluctuating in concert with their prey populations.

Changes in Reproductive Rates

David Lack (1968:180) was one of the first ornithologists to emphasize the impact of prey populations on breeding success and output of birds. He showed that clutch size of *Accipitrinae*, *Buteoninae*, *Milvinae* and *Striginae* all increase from equatorial Africa to mid-Europe and argued that this trend was due to food limitations associated with the length of the foraging period each day. Although owls do not fit the simplistic model implicating length of day (i.e., foraging period) in regulating reproduction, Lack (1968) gathered voluminous data to support his contention that breeding rates (age at first breeding, number of clutches and clutch size) in raptors and most other birds are regulated by food availability.

Extensive studies in Europe have documented the close relationship between prey populations and breeding success in tawny owls (*Strix aluco*). Southern (1970) and Hirons (1982) concluded that tawny owl breeding success was primarily dependent upon the abundance and availability of the owl's two main prey species, wood mouse (*Apodemus sylvaticus*) and bank vole (*Clethrionomys glareolus*). When rodent populations were exceptionally scarce, owls remained resident in exclusive territories, but none attempted breeding. In more recent work, Wendland (1984) found that the breeding success of tawny owls and the proportion of yellow-necked field mice (*Apodemus flavicollis*) in their pellets (an index to population size) exhibited the same three-year cycle.

The three-year vole cycles of *Fennoscandia* provide frequent opportunities for researchers to examine the relationship between food and reproductive success. Solheim (1984) observed dramatic changes in pygmy owls (*Glaucidium passerinum*) in the number of clutches, clutch size and number of fledglings with changes in vole populations. No breeding occurred in years when he trapped no voles. Breeding success of several other northern owl species varies with the abundance of *Microtus* spp. Peaks in Finnish great gray owl breeding all occurred during peak vole years (Mikkola 1983:208-209). Long-eared owls showed marked fluctuations in breeding populations and average clutch size, depending on the density of *Microtus* spp.(Mikkola 1983:227). Korpimaki (1984) also documented changes in the number of nesting pairs, mean clutch size and mean number of young produced by long-eared and short-eared owls in Finland, corresponding with changes in *Microtus* spp. populations.

Rusch et al. (1972) and McInvaille and Keith (1974) studied great horned owl populations near Rochester, Alberta during six years of the 10-year cycle in snowshoe hare (*Lepus americanus*) populations. During a period (1966-1969) when snowshoe hare populations increased seven-fold, the percent of the great horned owl pairs nesting increased from 20% to 100% (Rusch et al. 1972). The number of fledged owls increased from two to 15. During a longer period (1965-1971), McInvaille and Keith (1974) documented an increase from one to 16 breeding pairs of great horned owls as hare populations increased from 16 to 306 per 40 hectares.

Some of the most dramatic evidence for the impact of prey populations on reproductive rates in raptors comes from studies of the common buzzard (*Buteo buteo*) in Europe. As *Myxomatosis* virus spread through England in the 1950s, the numbers of rabbits declined dramatically. Dare (1961) observed that only half as many young fledged per nest by buzzards in areas where rabbits were scarce as in areas where they were abundant. Dare (1961) monitored the effect of the epidemic as it spread into Avon Valley, Devon in 1955 and eliminated rabbits from the area. Compared to 1954, prior to the epidemic, the number of resident buzzards declined 35% and the number of young fledged fell from 17 to zero. In a 10-year study of common buzzards nesting near Castell, Germany, Mebs (1964, *in* Newton 1979:353) observed increases in clutch size, brood size at fledging and the number fledged per nest with a five-fold increase in vole densities. Total nest attempts and the number of successful nests, however, did not vary.

Numerous studies have documented changes in reproductive success of ferruginous hawks associated with changes in the abundance of their prey (Howard and Wolfe 1976; Woffinden and Murphy 1977; Smith and Murphy 1978, 1979; Thurow et al. 1980; Smith et al. 1981; Steenhof and Kochert 1985). Howard and Wolfe (1976) observed a doubling of the number of young per pair in a year of high jack rabbit (*Lepus californicus*) numbers compared to a low year. On the Snake River Birds of Prey Area, Steenhof and Kochert (1985) documented a 65% decrease in the number of young fledged per nest attempt during a drought which drastically reduced the number of prey.

The response of raptors to changes in factors influencing prey availability has received less attention. Southern and Lowe (1968) demonstrated that tawny owl breeding success at Wytham Wood was higher on territories where bank voles were more available, regardless of prey densities. At the same study site Hirons (1985*a*) demonstrated how rainy weather during nesting reduces rodent availability, leading to reduced tawny owl nesting success. Factors influencing the raptor's access to prey, then, can have a direct influence on productivity regardless of prey densities.

Raptor Population Changes

One of the earliest studies of an entire raptor community and its prey was the pioneering work of Craighead and Craighead (1956). They observed a four-fold increase in raptors from one winter to the next, corresponding to a six-fold increase in meadow voles (*Microtus pennsylvanicus*) in the area. Rough-legged hawks and northern harriers increased particularly. Because of their mobility, raptors have the potential to respond quickly and dramatically to prey changes. Enderson (1964) found that the presence of prairie falcons in Colorado corresponded to the presence of horned larks (*Eremophila alpestris*), their main prey. Likewise, year-to-year differences in falcon density corresponded with differences in lark densities. Hamerstrom's (1979) 16-year study of harrier populations in central Wisconsin demonstrated a strong link between nesting numbers and vole abundance. Although many of these increases may have been due to movements, the higher wintering or breeding densities probably led to higher densities in the following seasons or years.

Galushin (1974) summarized many examples, primarily from the Soviet Union, in which changes in harrier, kestrel (*Falco tinnunculus*) and other raptor populations corresponded with changes in abundance of their prey. Newton (1979:65-80) summarizes many more recent examples of this phenomenon for hawks, buzzards and eagles.

Numerous authors have documented changes in owl populations corresponding to changes in their prey, including Rusch et al.'s (1972) and McInvaille and Keith's (1974) work on great horned owls and snowshoe hare and Hornfeldt's (1978) work on long-eared and Tengmalm's owls (*Aegolius funereus funereus*) and voles. One of the best demonstrations of this relationship is Korpimaki's (1984, 1985) recent work on Tengmalm's owl, long-eared owl, short-eared owl, kestrel and harrier, in which he showed highly significant correlations between abundance of each of these populations and vole densities.

Mass Movements of Raptors in Response to Prey Crashes

Lack (1954:204-211) summarized early information on mass movement of raptors in response to prey crashes and eruptions. He suggested that periodic invasions of goshawks, great horned owls, snowy owls and great gray owls in North America corresponded to cycles in their primary prey. Likewise in Norway, where goshawks and eagle owls (*Bubo bubo*) prey primarily on lemmings (*Lemmus* spp.), invasions of these raptors occur every four years in correspondence with the four-year cycle in lemming abundance (Lack 1954). More recent studies have also documented large movements and emigrations in response to low prey populations: Hanson (1971), Catling (1972), Mueller et al. (1977), Adamcik and Keith (1978), Bell et al. (1979) and Hayward et al. (1987).

The movement patterns demonstrated by these raptor populations in response to changes in prey depend on the life history of the raptor. The degree of diet specialization, nest site availability and predictability of prey populations all influence how a species responds to changes in prey populations. Lundberg (1979) discussed the varied response of three owl species in northern Europe to changes in prey densities. The highly territorial Ural owl (*Strix uralensis*), which exhibits a generalist diet, is sedentary, occupying its territory and defending its nest site throughout prey fluctuations but foregoing breeding during prey lows. The long-eared owl, a vole specialist, nests in abundant stick nests and is largely migratory. It avoids seasonal prey scarcity through migration and readily shifts breeding areas in response to prey abundance. Tengmalm's owl exhibits an intermediate strategy of partial migration. This vole specialist nests in limited tree cavities. During periods of adequate prey populations, both males and females occupy stable home ranges year-round. Prey scarcity, however, leads to nomadic movements by females while males remain sedentary, defending the nest cavity.

In summary, studies show that raptors respond quickly and readily to changes in prey abundance. Can we exploit this behavior as an additional tool for managing raptors via their prey? Three points must be evaluated to assess the feasibility of managing prey and prey habitat to enhance raptor populations: 1) Can we increase prey through habitat manipulations? 2) Can we increase prey through direct manipulations? 3) If we increase their prey, will raptor populations increase?

CAN WE INCREASE PREY THROUGH HABITAT MANIPULATIONS?

Despite the constant occurrence of habitat manipulations resulting from land management actions, biologists rarely take advantage of such opportunities to document effects on wildlife, especially long-term effects. Many land management practices unintentionally result in increased prey populations. One example is increased habitat and prey availability provided to ospreys in the western United States as a result of reservoir construction (Van Daele and Van Daele 1982; Henny and Anthony, in this volume). Vulture and kite populations have grown in many urban areas due to increasing numbers of garbage dumps (Newton 1979:67). Other studies have documented increased small mammal or bird populations following logging (Maguire 1983, Mannan and Meslow 1984, Kirkland et al. 1985, Monthey and Soutiere 1985), prescribed burning (Bock and Bock 1983) and rangeland chaining (Sedgwick 1981). Most studies, however, monitored populations for only one year following treatment.

An alternative to increasing prey abundance is increasing prey vulnerability or availability. Mowing hayfields, for example, may make voles more available to harriers, short-eared owls and common barn-owls. Likewise, clearcuts may increase the availability of voles and pocket gophers to great gray owls and red-tailed hawks, if adequate perches are maintained.

Although some habitat manipulations may increase prey or its availability, many management practices often change prey species composition. Declines in some species offset increases in others and the long-term impacts of such changes on the entire community are unknown. The change in forest structure following logging almost always alters community composition of both bird and small mammal communities (Hagar 1960; Kilgore 1971; Webb et al. 1977; Franzreb and Ohmart 1978; Kessler 1979; Medin 1985, 1986). Effective raptor management may involve working with land managers to minimize reductions in key prey species. Unfortunately, we know so little about prey species' habitat requirements, we can not predict the long-term outcome of most manipulations.

CAN WE INCREASE PREY THROUGH DIRECT MANIPULATIONS?

The potent rodenticides being used and tested today are amazingly effective, producing 70-100% mortality rates (Anthony et al. 1984, Matschke and Fagerstone 1984, Barnes et al. 1986, Byers and Merson 1986, Lewis and O'Brien 1986, Ross 1986, Zhi and Chang 1986). These compounds often result in significant mortality of non-target species as well as target species. The widespread use of these toxicants demonstrates our ability to decrease prey populations as most of these pests are key prey species for raptors. Decreased use of rodenticides wherever possible would benefit many raptors. Pesticide use on agricultural and forest lands also reduces prey abundance for insectivorous raptors, e.g., burrowing owls and flammulated owls.

Besides reducing direct causes of mortality on prey populations, we can also enhance prey populations through positive actions. Fish hatchery and game farm programs have produced dramatic increases in many prey populations. A visible example is the use of introduced salmon by bald eagle populations. While actions such as the introduction of Kokanee salmon (*Oncorhynchus nerka)* to some lake/river systems may not directly increase bald eagle populations, the abundant food during stressful periods of their lives, such as migration, may increase the eagles' survival rate.

By providing limiting resources, we can also increase prey. For example, we may be able to augment flying squirrel populations by providing nest sites in the form of nest boxes. For other prey populations, food or critical nutrients are limiting. By providing supplemental food, Cole and Batzli (1978), Sullivan and Sullivan (1984), Krebs et al. (1986*b*) and Bomford and Redhead (1987) documented increased small mammal populations or increased reproduction. Herbivores, from elephants (Weir 1972, 1973) to ungulates (Belovsky 1981, Belovsky and Jordan 1981) to rodents (Aumann 1965; Aumann and Emlen 1965; Weeks and Kirkpatrick 1978; Young, in this volume) are limited by dietary deficiencies in trace salts and metals. Salting, therefore, may increase populations of some small herbivores.

On the other hand, population dynamics of many prey species are notoriously unpredictable. The numerous theories proposed to explain small mammal population dynamics (McLaren 1971, Tamarin 1978, Halle and Lehman 1987) all seem supported by at least one study. Despite supplemental feeding that increased population sizes, Cole and Batzli (1978) and Krebs et al. (1986*a,b*) were unable to prevent population crashes in voles and hares, respectively. Many authors have also suggested that predation itself drives population cycles (Angelstam 1984, Lindstrom et al. 1987). In light of such variability, would we see lasting changes in prey populations following manipulations? Is there potential to worsen problems by increasing peak prey populations with resultant increased raptor populations which then are left with no food resources when the prey populations crash? Emphasis must be directed at increasing the minimum population levels of irruptive prey and increasing their stability. Experimental and theoretical studies suggest that providing a good interspersion of hiding cover and refuges with foraging habitat will help attain these two goals (Huffaker 1958, Tanner 1975).

IF WE INCREASE PREY POPULATIONS, WILL RAPTORS INCREASE?

Assuming we do increase prey populations, can we be sure raptor populations will increase? Earlier, we cited many examples of raptors tracking natural prey increases, but raptor response assumes other factors are not limiting the birds' populations. Inflexible territorial behavior limits some raptors despite abundant food. Territorial behavior limits red-tailed hawks (McInvaille and Keith 1974), tawny owls (Southern 1970, Hirons 1985*b*), kestrels (Newton and Marquiss 1986) and peregrine falcon populations (Ratcliffe 1962). Nest sites, especially for cavity- or cliff-nesting species, may limit other raptor populations, such as screech-owls (Van Camp and Henny 1975), boreal owls (Lundberg 1979) and kestrels (Newton 1979:72). In the past, pesticide contamination limited golden eagles (Lockie et al. 1969), peregrine falcons, bald eagles and ospreys (Hickey and Anderson 1968). Recently, despite abundant food provided by biologists, lead poisoning resulted in the death of several California condors, indirectly leading to the extirpation of the wild population (Pattee and Wilbur, in this volume).

Increasing prey abundance will also be ineffective for increasing raptor populations if prey are unavailable to the birds. Wakeley (1978) showed ferruginous hawks selected habitat by vegetation cover density rather than prey density. Provided at least some prey were present, hawks preferred areas free of cover and avoided dense cover areas despite high prey densities. Baker and Brooks (1984) also showed that red-tailed and rough-legged hawk densities did not always correspond with prey densities. The amount and distribution of cover influenced raptor distribution. Sonerud (1986) discussed migration strategy and habitat use of boreal raptors as a result of the interaction between life history and snow cover (i.e., prey availability). Species adapted to hunt in open habitats (e.g., short-eared owl, harrier and long-eared owl) were forced to migrate, even during peak vole years, when snow cover made prey unavailable. Resident species, on the other hand, were those with sit-and-wait tactics that could hunt in forests where prey were more available. Sonerud (1986) suggested great gray owl distribution was limited to areas with continental climate and soft snow where its snow plunging hunting tactic was effective. A hard snow crust made prey unavailable to the owls. For Tengmalm's owls, Sonerud (1986) documented seasonal habitat shifts that corresponded with changing prey availability due to snow and vegetation interactions. Southern and Lowe (1968) documented a relationship between breeding success and prey availability for tawny owls. The owls captured open habitat wood mice four times more often than the more abundant bank voles that inhabited dense cover. As a result, breeding success of pairs depended on the ratio of open/dense cover types.

RESEARCH RECOMMENDATIONS

There is a pressing need for research in the following areas:

- cooperative research with range ecologists, foresters and scientists studying prey population dynamics;
- long-term studies and monitoring of key prey populations and their raptor predators;
- properly designed experimental studies of the short- and long-term impacts of habitat manipulation on prey and raptor populations;
- evaluation of the potential for increasing the minimum population size of cyclic prey populations and the diversity of prey species in the ecosystem;
- development and testing of management strategies for stabilizing eruptive prey populations through increased habitat diversity or provision of refugia; and
- evaluation of the potential for increasing prey availability by burning, grazing, mowing, thinning, selective harvest or other habitat manipulations.

MANAGEMENT RECOMMENDATIONS

- We must carefully evaluate the potential impact on prey populations of any habitat management carried out for other purposes.
- For systems where there is sufficient information, we should make much greater use of habitat manipulations for the purpose of increasing prey populations. To do this we must work closely with range managers or silviculturists to develop prescriptions to accomplish specific goals.
- Prior to habitat manipulation we must define goals, identify target species and associated prey, and evaluate potential influences on non-target raptors and other members of the community.
- Manage habitats to increase prey availability, diversity or stability when these goals are more beneficial to raptors than increased prey abundance.
- Document effects of habitat manipulations on prey and raptor populations.
- Educate the public, land managers, our peers, and ourselves about our goals and needs when manipulating habitat to enhance prey populations.
- Eliminate the use of pesticides wherever possible.
- Reintroduce prey populations to patches of habitat from which they have disappeared.
- Work with managers of wildlife refuges and other land units where wildlife resources are primary products, to adjust timing and placement of agricultural activities.

CONCLUSIONS

Our ignorance of prey species' habitat needs and population biology makes management of their populations difficult. The strong tie between raptor populations and their prey, however, makes it difficult for us to effectively manage raptors without also managing their prey. Whether performed intentionally or inadvertently, land management activities will influence prey populations and, indirectly, raptors. Though difficult, management of raptor populations via their prey offers enormous potential.

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