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SYNCHRONOUS FLUCTUATIONS IN POPULATIONS OF SOME RAPTORS AND THEIR PREY

VLADIMIR M. GALUSHIN

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Despite brilliant analyses of raptor-prey interactions by Formosov (1934), Uttendorfer (1939), Errington (1946, 1963), Tinbergen (1946), Craighead & Craighead (1956) and others, the general ecological theory of predator-prey fluctuating systems has been based mostly on models involving carnivorous mammals, fish and insects. Sometimes there is no mention of raptorial birds, even in special chapters such as 'Predator-prey interactions' (MacArthur & Connel 1966), or 'Predators and predation' (Watt 1968). More often data on avian raptors have been used only as illustrations. As a result the well-known asynchronous or lagging type of predator-prey fluctuating system, mathematically worked out by Lotka (1925) and Volterra (1926), receives mention in book after book.

Yet one might suppose *a priori* that the unique mobility of birds could not have failed to affect their population dynamics. In view of this, a comparison of raptors with carnivorous mammals might be expected to bring to light some interesting differences. It is the purpose of the present paper to discuss the synchronous predator-prey fluctuations which seem to be characteristic of some raptor populations, as well as the classical Lotka–Volterra theory. It must be stressed, however, that the evidence on which the arguments are based is drawn from work on raptor populations in the Northern Palaearctic, mainly in the U.S.S.R. Evidence from Australia, Africa and America has been mentioned by Brown & Amadon (1968). Therefore the conclusions should not be taken as applicable beyond this region without additional studies.

A number of population studies of northern raptors show that the most marked annual fluctuations in numbers are found in open-country species whose food supply—mostly a relatively small number of rodent species—oscillates sharply from year to year. In the U.S.S.R. the Rough-legged Buzzard *Buteo lagopus* in tundra, harriers *Circus* spp. in steppe, and the kestrels *Falco tinnunculus* and *F. naumanni* in semi-desert are well-known examples. On the other hand, raptors whose diet is broad and/or rather stable show smaller fluctuations in number from year to year or do not fluctuate at all. The Peregrine Falcon *F. peregrinus* in tundra, Saker *F. cherrug* in steppe, and Short-toed Eagle *Circaetus gallicus* in desert, as well as a majority of forest birds of prey, are examples of this kind.

The stable raptor populations need not concern us further. As regards the raptorial birds and carnivorous mammals with oscillating populations, field studies—at least within open habitats of the North Palaearctic—show the existence of two types of fluctuations. The lagging (or asynchronous) type chiefly characterizes carnivorous mammals; its most distinctive feature is a one- or two-year time lag of the peaks and troughs of their population fluctuations those of their principal prey species. The coincident (or synchronous) type mainly characterizes raptorial birds; its most significant feature is the temporal coincidence of the peaks and troughs with those of the principal prey. Although ecologists have paid a great deal of attention to the asynchronous type, the no less interesting synchronous fluctuations also deserve to be discussed thoroughly.

EVIDENCE FROM FIELD STUDIES

The first evidence of this phenomenon in Russia appeared some 60 years ago (Sushkin 1908, Valkh 1914). The special study by Formosov (1934) contained a thorough analysis of his own data and the literature, which left no doubt as to the existence of synchronous population fluctuations of rodents and their avian predators. Later, many ornithologists who had worked in the open country of the northern (tundra) and southern (steppe and desert) belts of the U.S.S.R. emphasized the same (Osmolovskaya 1948, 1953, Dementiev 1953, Rustamov 1957, Gibet 1960, 1963, Sukhinin 1971, and many others). Data of the same kind for other European countries are summarized, for instance, by Glutz *et al.* (1971).

It is important to note that the area over which the fluctuations are synchronized in open country may be vast. In 1948, for instance, a drastic fall in rodent populations coincided with a sharp decrease (to a fifteenth of the previous year's levels) in the numbers of harriers, kestrels and other raptors over an area extending for hundreds of kilometres in northwest Kazakhstan (Gibet 1960).

In forested country, and in wooded steppe, the position is less clear-cut. There is some evidence for synchronization: for example, the annual fluctuations in the numbers of bank voles *Clethrionomys* and of kestrels at the Oka station (Ryazan District) are practically identical (Galushin 1971), and at the Vladimir station (Vladimir District) in 1964 an unusual abundance of Honey Buzzards *Pernis apivorus* coincided with a massive increase in wasps (Galushin & Kulukina 1969). On the other hand, changes in numbers of the Buzzard *Buteo buteo* at the Oka station were not so clearly related to changes in the numbers of rodents. It seems that the Buzzard is not affected unless the change in numbers of its prey is substantial, as Likhachev (1961) and Mebs (1964) have also found. Fluctuations in Buzzard populations in Britain, documented over half a century by Moore (1957), were mostly caused by anthropogenic factors.

It is noteworthy that in forest synchronous fluctuations of raptors and their prey have been detected in considerably smaller areas than in open country. Thus, in the Kalinin District, Belyakov (1964) found areas extending for several dozen kilometres that were characterized by the presence of large numbers of both rodents and birds of prey (Kestrel, Buzzard and Hen Harrier *Circus cyaneus*).

The existence of the synchronous type of predator-prey interacting system raised the question of the mechanism of synchronization. Some cases which cannot be explained in a traditional way by the processes occurring within the local raptor populations are given below.

In the autumn of 1957 the population of adult and young Kestrels at the Oka station was merely 10 birds while in the spring of 1958 the same area was populated by 22 birds. In the same area the respective figures for Honey Buzzard were as follows: autumn 1956, not more than 12 birds (even ignoring possible deaths among the young birds); spring 1957, 14 birds (Galushin 1971). No Honey Buzzards were registered in the area of the Vladimir station in 1963, but in the next year five pairs nested there (Galushin 1970). In the above years there was no noticeable reserve of non-nesting Kestrels or Honey Buzzards in the areas under observation.

In Tulskie Zaseky (Tula District, U.S.S.R.), the entire population of Buzzards in the autumn of 1940 was about 30–35 birds including non-breeders; in the next spring 56 birds nested within the area (Likhachev 1961).

In Berkshire (southern England) the total number of Tawny Owls *Strix aluco*, both adults and fledged young, within the 1000-acre Wytham Wood was 28 in summer 1951 while the next spring 34 owls nested there. The same area supported 12 owls in summer 1955 (minimum bank vole numbers); in spring 1956 (vole population increasing) as many as 46 owls started breeding (Southern 1959).

The only acceptable explanation for these cases is that some species of predatory birds are capable of undertaking more or less extensive nomadic movements within their breeding ranges in search of enough food for them and their future broods. This explanation was offered by Formosov (1934) and a little later by Uttendorfer (1939). Such nomadism is

similar to the invasions or eruptions of other species, except that the nomadic wandering of raptors normally takes place within the breeding range of the species.

For migratory raptor populations the process of synchronization with the state of their food resources is presumably one of spatial adjustment at the time of spring migration. From their wintering grounds the birds migrate north towards their breeding grounds, singly or in small groups. They may stop, sometimes for quite long periods to feed in areas where food resources are good, (Mayaud 1957, Varshavsky 1957). Some individuals, probably those breeding for the first time, may even stay in such areas and nest (Dorst 1962). Adult birds presumably return to their previous nesting territories but, if food is scarce there, some or all of them may move away in various directions, including back to the south (Gibet 1963). In this connection it may be mentioned that at the Oka station the pre-nesting period (the time from arrival to the beginning of laying) was found to be longer for raptors with unstable populations than for the more stable species. This may be an adaptation enabling the former to have time to assess the situation before attempting to breed.

Exceptionally, birds may shift beyond the normal breeding range. Thus seven pairs of Rough-legged Buzzards nested near Oslo in 1962, far to the south of their normal range where rodents were unusually abundant (Mysterud 1964). There are also records of species nesting well to the north of their usual range in similar circumstances: for instance, Kestrel in the Kola peninsula (Vladimirskaya 1948), and Pallid Harrier *Circus macrourus* in southwest Sweden (Lundevall & Rosenberg 1959).

The selective advantage of pre-nesting wandering, or 'searching migrations', in response to food shortage, seems clear. The numbers and biomass of most prey species are at a minimum in spring. The discovery of a substantial standing crop at this time is therefore a reliable indication that food will be abundant at the time when the young have to be fed. As man alters the face of the country at an increasingly rapid rate, these nomadic movements may become even more vital to the species which exhibit them.

EVIDENCE FROM RECOVERIES OF RINGED BIRDS

Ringing recoveries of birds of prey provide some supporting evidence. Using all the European literature available to me (about 220 titles published before 1965) and the card index of the U.S.S.R. Centre for Bird Ringing, I have checked over 6000 recoveries of predatory birds. Of these, only some 150 are suitable for analysis for the present purpose (Table 1), namely those in which the birds were ringed, (mostly as nestlings) in the breeding season and recovered in the breeding season at least two years later (see footnote to table).

Table 1 shows a wide range of distances between birth or nesting place and subsequent breeding area. I believe that it is not accidental that the upper half of the table (the more 'settled' species) includes the Sparrowhawk *Accipiter nisus*, Black Kite *Milvus migrans* and Goshawk *Accipiter gentilis* (the Osprey *Pandion haliaetus* would have come fifth on the list, at 82±53 Km, had there not been one, perhaps casual, vagrant from Sweden to Scotland). These are species which do not normally show population fluctuations. The species whose populations are known to fluctuate most markedly in particular areas, Kestrel, Montagu's Harrier *Circus pygargus*, Honey Buzzard and Rough-legged Buzzard, occupy the lower ('nomadic') half of the table.

Within a species, there may be differences in the degree of dispersal, as measured in Table 1, and such differences accord well with differences in the stability of the different populations. For example, in western and central Europe the distances between place of ringing and of recovery are notably shorter for Common Buzzard (60±11) and Kestrel (146±59) than in northern and eastern Europe (295±105 and 277±57 Km respectively). Perhaps the food resources of these two species fluctuate less in the west than in the east, but the more favourable climate in the west may also have some effect.

TABLE 1

Displacement in breeding territory of birds of prey

Species	Distance (km) from the place of ringing to the place of recovery (within breeding season) of raptors at the age of 2 years or above. Mean ± s.e.
Hobby *Falco subbuteo*	39±14
Sparrowhawk *Accipiter nisus*	41±21
Black Kite *Milvus migrans*	49±36
Goshawk *Accipiter gentilis*	60±16
Buzzard *Buteo buteo*	90±21
Osprey *Pandion haliaetus*	174±100
Marsh Harrier *Circus aeruginosus*	174±137
Kestrel *Falco tinnunculus*	192±43
Montagu's Harrier *Circus pygargus*	199±58
Honey Buzzard *Pernis apivorus*	997±375
Rough-legged Buzzard *Buteo lagopus*	1955±1079

Note: The inclusion in the table also of the presumably non-nesting yearlings, as was done in my preliminary note (Galushin 1964), changes the general picture little, though on the whole the distance of displacement is normally greater.

It must be stressed that the figures given in Table 1 should be regarded as preliminary, and as suggestive rather than conclusive, since the samples are small and the standard errors very large. Nevertheless the general trend seems clear.

EVIDENCE FROM SYSTEMATICS

Indirect—and, certainly, less reliable—evidence for differences in the amount of dispersal between various raptorial species is provided by their systematics. It is known that, in general, the extent of subspecific differentiation varies inversely with the degree of wandering or dispersal (Mayr 1947, White 1959). On this basis one would expect the species showing least dispersal to have the greatest number of subspecies, and vice versa. The actual situation is in fact close to expectation. According to Brown & Amadon (1968) most subspecies—7–17 for whole range, or 3–8 for Northern Palaearctic (Vaurie 1965)—are found in Peregrine (17 *in toto*, 8 within the Northern Palaearctic), Black Kite (7, 3) and Marsh Harrier *Circus aeruginosus* (8, 3). Other harriers (1–2, 1), Lesser Kestrel (1), Red-footed Falcon *Faco vespertinus* (2, 2), Imperial Eagle *Aquila heliaca* (2, 2) and Steppe Eagle *A. nipalensis* (2, 2), Long-legged Buzzard *Buteo rufinus* (2, 1), Rough-legged Buzzard (4, 3) and Honey Buzzard (1) are either monotypic or are represented by 2–4 subspecies (1–3 the Northern Palaearctic). There are of course exceptions: for instance the small number of subspecies in the Hobby *Falco subbuteo* (2, 1), Osprey (5, 1) and Short-toed Eagle (4, 1), and the rather large number of subspecies in the Kestrel (11, 7). But other factors are obviously involved in subspeciation besides mobility; for instance some of the Kestrel subspecies are insular populations and well isolated geographically, whereas the vast territory of the Northern Palaearctic is inhabited almost entirely by the nominal form.

DISCUSSION

CONJUGATE EVOLUTION OF FOOD SPECIALIZATION AND NOMADIC ABILITY

The facts and arguments given above lead to a consideration of the evolutionary connection between nomadism and food specialization. At its simplest, nomadism may compensate to some extent for insufficient trophic flexibility. Ghilarov (1954, 1961) has developed this idea with respect to insects. The alternative strategy is to be conservative with regard to territory and flexible with respect to food. Both evolutionary trends are

found in raptors. In brief, some birds of prey have evolved the ability to change food within permanent nesting territories, others to change territories in search of a particular food (Galushin 1964, 1966).

It should be noted that the distinction between the two alternative strategies may be traced not only in comparisons between species but also in different geographical populations of the same species, and even, on occasion, at the individual level. Thus those individuals that remain in an area where a particular food is scarce may survive by broadening their diets, as has been found for Buzzards in forests at Vladimir Station (Likhopeck 1970).

Individual specialization in feeding habits has been regarded as the first stage, the very beginning of the emergence of new forms. These views have, for instance, been expressed by Schwarz (1947) with respect to the Lesser Kestrel, or in more general form by Voous (1969) for the buteonine complex in Surinam. Against this, it has been argued that the constantly changing environment would not allow such specializations to persist and become hereditary (Krivonsov 1963). But this objection loses some of its force if one takes into account the territorial plasticity of some raptorial birds. Nomadism in search of food represents an active method of selecting favourable living conditions and one that must enhance the possibility of food specialization, with its all behavioural, physiological and morphological consequences.

DIFFERENCE BETWEEN NOMADISM IN RAPTORS AND EMIGRATION IN OTHER PREDATORS (CONSUMERS)

It is self-evident that the level of any local animal population is determined by the combined effects of reproduction, mortality and movements (immigration and emigration). In Soviet ecological literature N. Naumov (1958, 1963) has most fully discussed the interaction of these three factors, and has developed the concept of 'biological momentum', which is widely held as being applicable to predator-prey systems. According to this idea, a favourable food situation—that is, the abundance of a producer, or prey species—leads to the increase of the consumer, or predator population, as a result of its higher reproduction and reduced mortality. A surplus is thus created in the predator population, which may be aggravated by the reduction of the prey population in the following breeding season. The consequent imbalance between predator and prey results in the emigration of a part of the predator population, mainly young individuals. Emigration thus acts as a kind of safety valve through which surplus individuals are removed from saturated populations. In such a system the fluctuations of a predator population will be of the asynchronous or lagging type, referred to earlier.

The existence of the asynchronous type of predator-prey fluctuations has been repeatedly confirmed among carnivorous mammals, especially in the north (Butler 1953, and many others). In such cases emigration away from saturated areas results from the local disproportion between the stock of food and the number of consumers. Emigration is likely to be relatively slow and more or less accidental in direction, and those taking part will tend to be the less experienced individuals. It would therefore be expected that losses will be high among emigrants, and there is in fact evidence that this is so.

The pre-nesting 'probing' migrations of raptors are of quite a different nature. They may indeed be thought of as adaptations leading to the elimination, or at any rate the reduction, of what one may call the 'non-productive' losses of post-nesting surplus emigrations. They tend to balance the local populations of predators with their food resources before the disproportion between them can appear. Since they take place at the time of normal pre-nuptial migrations, simply making them longer or shorter, these nomadic movements presumably do not lead to significant additional mortality. Furthermore, they enhance the chances of survival of the migrants' offspring.

Therefore the basic thesis of this paper is the recognition of the mobility of some raptorial birds as the main instrument for matching their population levels in each reproductive season to the state of the food resources within any area. In such a situation raptor nomadism emerges not as a consequence of the disbalance in a consumer-producer (predator-prey) system, but as an effective, though not absolute, means to prevent it.

COMPARISON WITH ASYNCHRONOUS FLUCTUATIONS OF CARNIVOROUS MAMMALS

The active role played by nomadic 'probing' migrations of raptors constitutes a basic difference in the population dynamics of those predatory birds and carnivorous mammals in unstable food resources. The ability of the birds to redistribute their population within the breeding range, in accordance with the availability of food, should enable them to maintain a steadier annual reproductive output and more stable total populations than those of carnivorous mammals. Indeed, if the arguments developed here are valid, raptor populations should consist of a more or less constant number of individuals which shift within a large area, whereas carnivore populations should show continual fluctuations in total numbers. In both cases there will be local fluctuations but the causation will be different, and in the raptors they will be synchronous with fluctuations in prey numbers while in the carnivores they will be asynchronous.

Hence it would be logical to expect a higher fecundity in carnivorous mammals than in raptorial birds, to counteract the higher mortality. A high fecundity ensures that the species will always be able to take full advantage of favourable conditions that may develop. Although the systematic groups compared in this way appear to be remote, important differences are apparent in fecundity between some raptors and carnivores. For example, the fecundity of the Arctic Fox *Alopex lagopus* is twice as high as that of the Rough-legged Buzzard, which exploits a similar food supply but is much smaller in size.

Of course the difference between raptors and carnivorous mammals in this respect is not absolute: 'searching migrations' are not a monopoly of the former, nor is high and variable reproductive output a monopoly of the latter. Both these phenomena play a certain, but not equal, part in the population dynamics of these groups. Other factors, some of them conflicting with the generalizations just made, must be taken into account, such as the variability of clutch-size and the number of clutches in owls and some birds of prey; cannibalism as a means of control of the number of young depending on the availability of food (Ingram 1959); the migrations and invasions of Arctic Fox, Wolf and other carnivores in response to food shortage. Group behaviour (Chauvin 1969) probably also plays a role in the population dynamics of both groups. Furthermore, if a general decrease in the prey population affects the entire nesting range of some raptor species, the population of the latter will begin to show the lagging type of fluctuation; but this extreme case need not be discussed in detail.

ENERGETIC ASPECTS

The two contrasting adaptations, discussed above, may be looked upon as alternative methods of coping with the problem of food supply. The realization of either of these adaptations will require a certain amount of expenditure of energy, in the one case in movement (flight) and in the other case in reproduction. One is reminded in this connection of the conclusion reached by Schwarz (1963) on the close-to-stress state of the energy balance of high-fecundity species. It is also well known that a high consumption of energy is required for bird migration (Dorst 1962, Dolnik 1970). There is scope for research into the evolution of energetic strategies.

SUMMARY

Raptorial birds which depend on a small number of prey species, especially those living in open habitats in the tundra, semi-desert and desert belts of the Palaearctic, undergo local fluctuations in numbers which are synchronous with the fluctuations in numbers of their main prey species. In this they contrast with the asynchronous or lagging type of predator-prey oscillation which has received wider attention in the literature.

Evidence from ringing recoveries shows that the species which fluctuate locally in synchrony with their prey tend to move greater distances from their birth-place or previous breeding place than those with more stable populations. The former species also tend to be split into fewer subspecifically distinct forms than the latter. It is argued that the species which are subject to a fluctuating food supply have evolved, as an important adaptation, the ability to undertake more or less extensive 'searching migrations', which enable them to find and settle in areas of adequate food supply, often far removed from the previous breeding area. In the longer evolutionary aspect, this ability may be a factor promoting food specialization.

The synchronous population fluctuations of raptorial birds with their prey are compared with the asynchronous or lagging oscillations of carnivorous mammals.

REFERENCES

BELYAKOV, V. V. 1964. (The number and territorial distribution of birds of prey in the Kalinin District). Uchen. Zap. kalinin. Pedagog. Inst. 31: 20–40. (In Russian.)

BROWN, L. & AMADON, D. 1968. Eagles, hawks and falcons of the world. London: Country Life Books.

BUTLER, L. 1953. The nature of cycles in populations of Canadian mammals. Can. J. Zool. 31: 242–262.

CHAUVIN, R. 1969. Le comportement animal. Paris: Masson.

CRAIGHEAD, J. J. & CRAIGHEAD, F. C. 1956. Hawks, owls and wildlife. Wildlife Management Institute, Washington, D.C.

DEMENTIEV, G. P. 1953. (Predatory birds reproduction and number of rodents in North-Eastern Turkmenia). Byull. Mosc. Obshch. Ispÿt. Prir. (biol.) 58: 15–20. (In Russian.)

DOLNIK, V. R. 1970. Physiology of migratory state: a comparison of migratory and sedentary races. Abstracts, 15 Int. Orn. Congr.: 14–15.

DORST, J. 1962. The migrations of birds. London: Heinemann.

ERRINGTON, P. L. 1946. Predation and vertebrate populations. Quart. Rev. Biol. 21: 144–177.

ERRINGTON, P. L. 1963. The phenomenon of predation. Am. Scient. 51: 180–192.

FORMOSOV, A. N. 1934. (Raptors and rodents). Zool. Zh. 13: 664–700. (In Russian.)

GALUSHIN, V. M. 1964. (The nature of synchronization of population dynamics of predators and their prey). Sovremennye problemy izuchenia dynamiky chislennosty populatsiy zhivotnikh, Moskva: 24–26. (In Russian.)

GALUSHIN, V. M. 1966. (Synchronous and asynchronous types of motion of the predator-prey system). Zh. Obshch. Biol. 27: 196–208. (In Russian.)

GALUSHIN, V. M. 1970. Ecological and economic effects of birds of prey in the Central Region of the European Part of the U.S.S.R.—with special reference to the 'Index of predatory pressure' as a means of estimating this effect. I.U.C.N., 11th Technical Meeting, Morges, Switzerland: 166–174.

GALUSHIN, V. M. 1971. (The number and territorial distribution of birds of prey in the Central Region of the European Part of the U.S.S.R.). Trudy Okskogo Zapovednika 8: 5–132. (In Russian.)

GALUSHIN, V. M. & KULUKINA, N. M. 1969. (The ecology of Honey Buzzard in the Vladimir District). Uchen. Zap. moskov. Pedagog. Inst. 362: 110–118. (In Russian.)

GHILAROV, M. S. 1954. (Species, population and biocenosis). Zool. Zh. 33: 769–778. (In Russian.)

GHILAROV, M. S. 1961. Einige Probleme der zeit-genossischen Biozönologie and ihre Lösung bei agrarentomologischen Studien. Beitr. Ent. 11: 241–255.

GIBET, L. A. 1960. (The number of birds of prey and its relationship with rodents in the steppe zone of North Kazakhstan). Ornitologiya 3: 278–291. (In Russian.)

GIBET, L. A. 1963. (Territorial peculiarities of population fluctuations of predatory birds). Byull. mosc. Obshch. Ispÿt. Prir. (biol.). 68: 42–49. (In Russian.)

GLUTZ VON BLOTZHEIM, U. N., BAUER, K. M. & BEZZEL, E. 1971. Handbuch der Vögel Mitteleuropas, Band 4. Frankfurt am Main: Akademische Verlagsgesellschaft.

INGRAM, C. 1959. The importance of juvenile cannibalism in the breeding biology of certain birds of prey. Auk 76: 218–226.

KRIVONOSOV, G. A. 1963. (Sketches on the ecology and geographical distribution of birds of prey in the Volga delta). Trudy Astrakhan. Zap. 8: 245–293. (In Russian.)

LIKHACHEV, G. N. 1961. (The nesting of Buzzard (*Buteo buteo*) in Tulskie Zaseky). Trudy prioksko-Terras. Zap. 4: 147–225. (In Russian.)

LIKHOPECK, E. A. 1970. (Tropic links of Buzzard in forest habitats). Nauch. Dok. Vyssh. Shkoly, Biol. Nauki 8: 21–24. (In Russian.)

LOTKA, A. J. 1925. Elements of physical biology. Baltimore: Williams & Wilkins.

LUNDEVALL, C. F. & ROSENBERG, E. 1955. Some aspects of the behaviour and breeding biology of the Pallid Harrier (*Circus macrourus*). Proc. Int. orn. Congr. 11: 599–603.

MACARTHUR, R. H. & CONNEL, J. H. 1966. The biology of populations. New York: Wiley Int.

MAYAUD, N. 1957. La migration 'en boucle' du Faucon Kobez, *Falco vespertinus* (L), en Afrique du Nord of Mediterranée. Alauda 25: 24–29.
MAYR, E. 1947. Ecological factors in speciation. Evolution 1: 263–288.
MEBS, T. 1964 Über Wanderungen und bestandsgestaltende Faktoren beim Mäusebussard (*Buteo buteo*) nach deutschen Ringfunden. Vogelwarte 22: 180–194.
MOORE, N. W. 1957. The past and present status of the Buzzard in the British Isles. Br. Birds 50: 173–197.
MYSTERUD, I. 1964. Fjellvåken, *Buteo lagopus* (Pont.), som hekkefugl pa lavlandet i 1962. Sterna 6: 7–26.
NAUMOV, N. P. 1958. (Some basic problems of the animal population dynamics). Zool. Zh. 37: 659–679. (In Russian.)
NAUMOV, N. P. 1963. (Animal ecology). Moscow. (In Russian.)
OSMOLOVSKAYA, V. I. 1948. (Ecology of raptors in Yamal Peninsula). Trudy Inst. Geogr. Akad. Nauk S.S.S.R. 41: 5–77. (In Russian.)
OSMOLOVSKAYA, V. I. 1953. (Geographical distribution of raptors in Kazakhstan plains and their importance for pest control). Trudy Inst. Geogr. Akad. Nauk S.S.S.R. 54: 219–307. (In Russian.)
RUSTAMOV, A. K. 1957. (Fluctuations in number of some birds of prey and their food specialization). Trudy turkmen. Sel'khoz. Inst. 9: 427–433 (In Russian.)
SCHWARZ, S. S. 1947. (Specialisation of the diet in Lesser Kestrel). Priroda 8: 66–67. (In Russian.)
SCHWARZ, S. S. 1963. (Ways of adaptations of terrestrial vertebrata to the living conditions in the Subarctic, Vol. 1, Mammals). Sverdlovsk. (In Russian.)
SOUTHERN, H. N. 1959. Mortality and population control. Ibis 101: 429–436.
SUKHININ, A. N. 1971. (Ecology of owls and raptors in Badkhyz, South-Eastern Turkmenia). Ashkhbad. (In Russian.)
SUSHKIN, P. P. 1908. (Birds of Kirgiz Steppe). Moscow. (In Russian.)
TINBERGEN, L. 1946. Die Sperwer als roofijand van zangvogels. Ardea 34: 1–213.
UTTENDÖRFER, O. 1939. Die Ernährung der deutschen Raubvögel und Eulen und ihre Bedeutung in der heimischen Natur. Nendamm: J. Neumann.
VALKH, B. S. 1914. (Concerning the expected invasion of mice and measures of their control). Byull. Vred. Sel'khoz. 2: 33–44. (In Russian.)
VARSHAVSKIY, S. N. 1957. (Seasonal nomadic movements and migrations of birds—mainly raptors—in the areas to the North of the Aral Sea). Trudy 2 Pribalt. Orn. Konf.: 69–84. (In Russian.)
VAURIE, C. 1965. The birds of the Palearctic fauna. Non-passeriformes. London: Witherby.
VLADIMIRSKAYA, M. I. 1948. (Birds of the Lapland Reserve). Trudy lapland. Zap. 3: 171–245. (In Russian.)
VOLTERRA, V. 1926. Variazioni e fluttuazioni del numero d'individui in specie amimali conviventi. Mem. Acad. Lincei 2: 31–113. (English translation in J. Conserv. Intern. Explor., 3: 3–51, 1928.)
VOOUS, K. H. 1969. Predation potential in birds of prey from Surinam. Ardea 57: 117–148.
WATT, K. E. F. 1968. Ecology and resource management. A quantitative approach. New York: McGraw-Hill.
WHITE, C. M. N. 1959. Nomadism, breeding and subspeciation in some African larks. Bull. Br. Orn. Club 79: 53–57.

Vladimir M. Galushin, Zoology Department, Moscow-Lenin State Pedagogical Institute, Kibalchicha 6, *Moscow* 1-243 *U.S.S.R.*