

painopiste oli lähinnä maan itäosissa ulottuen aina Suomenlahdelle saakka (VÄLIKANGAS 1930). Tämä invaasio oli yksilömäärältään suurempi kuin vv. 1959 ja 1962 invaasiot.

Sekä v. 1959 että v. 1962 Pohjois-Atlantilla vallinneet myrskyt painoivat muuttomatkaltaan oleita pikkukajavia Norjan ja Ruotsin tuntureiden yli Suomeen saakka.

Invaasioiden aikana löydetystä kuolleista yksilöistä on määritetty ikä joissakin tapauksissa, jolloin on saatettu havaita, että linnut ovat joko sellaisia nuoria lintuja, jotka olisivat pesineet k.o. vuonna (1959), tai vanhoja lintuja (1962).

Maassamme vv. 1928—61 havaitut muut yksilöt (11 kpl) olivat suurimmaksi osaksi (kaikki ikäsuhteiltaan ilmoitetut) nuoria yksilöitä, jotka ovat satunnaisesti tänne joutuneita harhailijoita. Ei myöskään tässä tapauksessa ole siis kysymys säännöllisestä muutosta, vaikka yksilöt onkin havaittu muuttoaikoina.

Tarkastelu johtaa siis tulokseen, että pikkukajava ei esiinny Suomessa (eikä ilmeisesti yleensääkään Itämeren piirissä) säännöllisenä muuttajana vaan satunnaislajina. Satunnaisesti esiintyneet yksilöt ovat kuuluneet kahteen eri kategoriaan:

1. imatureihin harhailijoihin, joita tavataan yksittäisinä yksilöinä sekä syksyllä että keväällä
2. sukukypsiin lintuihin, jotka ollessaan kevätkuutolla ovat joutuneet joukoittain myrskyn ajamiksi harhautuen normaailta muuttoreitiltään.

Significance of interspecific and intraspecific bird calls in the predator-prey relation¹

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With the help of experiments arranged with attraps, many important results elucidating the instinctive behaviour released by visual stimuli have been yielded in the field of modern ethology. Innate defence reactions for avoiding danger from the natural enemies of the species play a very central rôle among these instinctive functions. The well-known experiments with hawk-goose models releasing a fear reaction when sailed the short neck first are classic in the field.

In describing these reactions »innate» we mean that they are instinctive activities not based on learning, which are immediately discharged in response to certain comparatively simple combinations of stimuli. The above mentioned experiment with a hawk-goose model, for instance,

¹ This article was first published in Finnish under the title »Lajinvällisten ja lajinsisäisten äänyhteyksien merkityksestä peto-saalisuhteessa» in »Luonnon Tutkija» Vol. 56, Part 5 (1952). The author has slightly abridged the English translation and furnished it with comments (see p. 100). — The editor.

shows that the combination of stimuli consists of two parts, viz. the shape of the model and the direction of its movement. This relative simplicity also holds true for the visually perceived colour patterns (so-called recognition marks) which help to keep together animals living in herds or birds migrating in flocks, and which also help the young to follow their parents. Many woodland mammals living in herds have a clear white patch on the hind quarters or on the lower side of the stubby tail. Many of the light colour patterns in birds, so important to field ornithologists in species identification, are usually rather simple but very characteristic patterns serving for species recognition. They have been appropriately called »white-marks» or »white-signs» (valko-merkit) by a Finnish field-naturalist (RENVALL 1929).

In this article we are mainly interested in those instinctive reactions whereby prey animals defend themselves against danger from their enemies. Within each balanced community each species is perpetually menaced by the same enemies against which it must be prepared for defence in some measure, i.e. it must be sufficiently capable of avoiding its enemies. For this purpose those instinctive functions which are based on »recognition» of the enemies and on the defensive movements (or motionlessness) automatically resulting from it undoubtedly play a central rôle, in addition to the means of passive protection (protective colouring, camouflage).

The above mentioned experiments with attraps show that the birds recognize their enemies by sight. This is very clearly shown in the wellknown use of a mounted horn-owl (*Bubo bubo*) in the destruction of crows. Every field-ornithologist also knows how birds behave and how they utter sounds on seeing a flying bird of prey. These are so characteristic that a mere glance from a forest clearing is enough to confirm the observer of the presence of a silently flying hawk.

Although the visual recognition of enemies by birds and other animals is well known, our knowledge of the significance of sign stimuli perceived by ear is much more scanty. Recent investigations, however, have shown that auditory recognition and instinctive behaviour as an innate reaction to certain sounds functioning as sign stimuli also play an important part among the defence mechanisms of animals. It has been shown in the case of insects that the ultra sounds used by bats for echolocation in catching moths result in a distinct fear reaction in the latter (SCHALLER and TIMM 1950, quoted by SUOMALAINEN 1951). Good evidence of the results of natural selection in the formation of defence mechanisms

of this kind has been gained also from studying the ability of birds to recognize their enemies. It has been shown experimentally (MILLER 1952) that small species do not react to the calls of large owls, while those that are large enough to be preyed upon by them at some stage of their life react immediately. On the other hand, small species react to sounds emitted by small owls. These experiments have also revealed that a species which reacts strongly to the calls of its raptorial owl within their common area, does not usually react to it within those parts of its range which lie outside the native area of that owl.

As these functions are based on the innate power to react to the calls of a particular predator belonging to the regular enemies of the species in question, we can thus speak with MILLER (op.c.) of »racial experience» peculiar to an individual species or even to an individual population within the species. This »experience» is an automatic consequence of eliminating by selection those individuals not possessing this power. Within the areas where the predator is not met with, no selection of this kind has taken place and, consequently, the predator is not recognized by its otherwise regular prey animals there. This recalls the numerous cases where morphologically similar closely related species living in the same area possess distinctly different call-notes and songs as specific recognition signals, but this difference is much less or totally lacking in the populations living away from those of the related species.

An observation by the author (VOIPIO 1952) on the green sandpiper (*Tringa ochropus*) reveals the many-sidedness of the auditory communications which are significant for the predator-prey relation and thus brings an interesting contribution to the discussion of these questions. It indicates, first, that these auditory communications not only concern the relation between the predator and its prey, but also function as alarm mechanisms between the young and the parent. The young probably first reacts to the stimulus perceived by sight, and the parent in turn to the sound of its young. In the case of the green sandpiper, the young obviously uttered sounds on first coming into touch with my hand. But it is possible, judging from the behaviour of the parent, that it does so also on seeing the enemy. Man is presumably not the regular enemy of the green sandpiper with which the species had become acquainted, but as the study by MILLER (1952) mentioned above shows, certain strange tone qualities in sounds do produce alarm reaction. The same may also be true of the unusual impressions perceived by sight.

Secondly, it is particularly noteworthy that the alarm note uttered by the young of the green sandpiper approaches the upper hearing limit of the human ear. A cry of this kind, though audible to the natural enemies of the species, is thus disguised to a certain extent, or in other words, is difficult to locate. We know from experience how difficult it is to locate the high pitched call-notes of certain birds (e.g. those of the goldcrest).² Sounds which are relatively difficult or impossible to locate by the enemy, but whose origin is easily located by the parent³, are particularly important, of course, for the safety of the brood. The attention of the enemy moving on the ground is by necessity fixed upon the parent who, alarmed by the cries of the young, frantically flies round it and screeches loudly. Such a defence mechanism is, of course, most effective in those instances where the enemy does not hear the cry of the young at all. Such is the case, for example, in man who cannot hear the cry of the beaver young, whereas its mother reacts to it from a long distance.

Such observations lead to the following interesting conclusion: the auditory communications serving as recognition signals, for instance, between morphologically similar closely related species *must be* clearly audible to function as part of the isolating mechanism but the communications between the young and parents (perhaps also between individuals moving in flocks) *must not* be so audible that they can be easily located.

We are now aware of the formation of colour patterns, shapes and sounds, the distinctness of which is the condition for their perfect functioning as sign stimuli for the releasing mechanism in other individuals of the same or another species. Much discussion has centred round their evolutionary significance (see e.g. HUXLEY 1942) but no attention seems to have been paid so far to those auditory communications that essentially function as calls difficult to locate. Though the auditory recognition signals serve to keep the groups apart (e.g. the song of the related species) because of their distinctiveness, they seem also to act as sounds difficult to locate or even inaudible to the individuals not belonging to the species (e.g. many birds moving in flocks).⁴ The fact that the alarm calls uttered by many bird species on observing a flying hawk are very high pitched and difficult to locate, at least for the human ear, may also be no mere chance but probably represents defence mechanisms developed by different species with the aid of natural selection.

Comments

² This point deserves a comment, however, which is not necessarily an argument against the supposition that these contact notes function as disguised calls. They certainly do not possess all the characteristics (high pitch, long duration, no sudden changes in pitch, beginning and end gradual, not rhythmically repeated) which make some of the bird calls (e.g. alarm calls on seeing a hawk) particularly difficult to locate (see THORPE 1961). They are, however, high pitched and repeated at irregular intervals by the members of the dispersed flock moving continually through the trees. The calls seem to come from all directions (e.g. those of the titmice, see VOIPRO 1952, p. 65). This is due, first, to their high pitch which makes location by phase-differences difficult, and in addition, their small wavelength results in free reflection from the trunks and branches of trees. Secondly, the calls of individual birds are so mixed that it is considerably more difficult to locate the source of single calls. In other words, though these contact calls are of relatively brief duration their mingling and coming from different directions does not even allow time comparison to be used for location. MARLER (1955, 1956) has also pointed out that certain other passerine species possess social calls which are difficult to locate (see also comment 3). Though the contact calls principally speak to the members of the own species («die Flugrufe sprechen — in erster Linie die eigene Art an», THIELCKE 1961, p. 288) and possess elements which make them function partly as specific recognition signals, they are yet «understood» by different species probably because of the elements of high frequency common to different species. The mixed flocks of titmice which attract the goldcrests and the tree creepers are indicative of this.

³ THORPE (1961, p. 32), in quoting my description of the observation made on the green sandpiper, questions whether the parent bird (if she did not know the position of the offspring already) was really able to locate the high-pitched sound «which one would have thought would have been hard to locate whatever the aural equipment of the bird might be». During the ten years which have elapsed since the time of describing this observation, our knowledge of the hearing of birds has grown considerably, and the new methods of analyzing song and call structures with the aid of sound spectrographs have revealed more precisely than before what is heard and how it is heard as well as how the structure of the calls is correlated with their function. This is briefly summarized by PUMPHREY (1961). Most important from our point of view, is the conclusion that the ability of birds to determine the direction of a sound is comparable with that of man and is determined and limited by the physical nature of the sound in the same sort of way. As regards the observation in question this should mean that a sound of this sort emitted by the young cannot be located by its parent. The adult bird reacted, however, to the call of the young even when the latter was held out of sight of the parent and after having been carried some meters away from the original point (VOIPRO 1952). As it must be very doubtful that the bird could locate its young from the position of the enemy which carried it, the only possible conclusion must be that the parent's swooping to the spot as a response to the cry of its young was directed against the enemy only, irrespective of the site of the young.

On the other hand, as pointed out by MARLER (1955), some species possess social calls (contact calls) which are difficult to locate or which «give few location clues to predators» (op.c., p. 7). In addition, many juvenile Passeres have calls which are difficult for man to locate and resemble the hawk call as shown spectrographically by MARLER (op.c.). This doubtless holds true for many other bird groups. Such is the case for instance with some shore birds whose chicks have a food begging call which gives only few directional clues. As pointed out

by my amanuensis, Mr. M. SOIKKELI, MA in discussing the matter, the chicks of the dunlin (*Calidris alpina*), for instance, emit sounds which can be roughly located as regards direction, while the distance estimation remains quite imperfect.

All these experiences show convincingly that many birds emit sounds which have to function as contact calls for different purposes (flock integration or social calls, food begging calls) and must thus be located by the other members of the species or by the parents, but yet be disguised to the human ear and presumably also to the enemies of the species. There are some gradations between sounds which are comparatively easy to locate and those which are not. In addition, it has been shown (THORPE 1961) that some owls are sensitive to tones above the mid-point of the voice of song birds. This is perhaps connected with their hunting by auditory equipment responding to the high pitched squeak of mice. And finally, rather high pitched sounds may begin and end abruptly enough to make possible the comparison of time differences. Thus, in conclusion, the possibility cannot be excluded that in the case of the green sandpiper also, the parents do locate their offspring even though the sounds they emit are hardly perceived by enemies or are extremely difficult to locate.

⁴ Later, in connection with investigations performed with sound spectrographs, the conflict between these different needs has been emphasized by MARLER (1955) who has greatly enlarged the concept of the sound structures in relation to the function they have to fulfill. It is interesting that MARLER (1955, 1956) also calls attention to the parallelism between animal coloration and vocalization where these different needs are manifest in both and stresses the adaptive nature of the structural differences of animal sounds serving for different purposes.

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Selostus: Lajienväliset ja lajinsisäiset ääniyhteydet linnuilla ja niiden merkitys peto-saalissuhteessa

Tämän aikaisemmin suomenkielisenä julkaistun kirjoituksen (Luonnon Tutkija 56, 1952) tarkoituksena oli kiinnittää huomiota lintujen ja myös nisäkkäiden eräisiin ääniin, jotka ovat niin korkeat, että niiden lähettä on vaikeata, ellei mahdotonta, paikallistaa. Tämä koskee monia parvina liikkuvia lintuja sekä niitä varotusääniä, joita lukuisat eri lintulajit päästelevät nähdessään lentävän petolinnun. Metsäviikolla tehty havainto, jota on selostettu toisessa yhteydessä (Voipio 1952), osoittaa lisäksi, että sama ilmiö on todettavissa myös poikasen ja emon keskeisessä, kuuoastimen välityksellä tapahtuvassa tiedottamisessa. Myöhemmät tällä

alalla suoritettut tutkimukset ovat antaneet aiheen palata kysymykseen ja esittää alkuperäisen kirjoitus hieman lyhennettynä englanninkielisenä versiona ja varustaa se huomautuksilla, jotka koskevat osaksi eräitä uusia tuloksia, osaksi sellaisia tutkimustöitä, jotka uusin menetelmin ovat vahvistaneet aikaisempien havaintojen pohjalla tehtyjä johtopäätöksiä.

Erityisesti äänispektrografien avulla suoritettu lintujen laulun sekä kutsu- ja varotusäänten analyysi on aikaisempaa täsmällisemmin selvittänyt, mitä linnut kuulevat ja miten ne kuulevat sekä miten äänten rakenne on korreloitunut niiden tehtävään. Nämä tutkimukset ovat ensiksikin osoittaneet konkreettisesti, että lintujen äänten rakenteellinen sopeutuminen tehtäväänsä todella on kahtalainen: joko niiden tehtävänä on helpottaa paikallistamista tai niiden tarkoituksena on tehdä se mahdollisimman vaikeaksi. Kysymys on siis äänten struktuurin adaptiivisesta sopeutumisesta erilaisiin tehtäviin ja siitä, että eräät äänet (esim. korkeat varotusäänet lentävän haukan lähellä ollessa) ovat samansuuntaisesti vaikuttavan vallinnan ansiosta itsenäisesti kehittyneet eri lajeilla rakenteeltaan samanlaisiksi. Toiseksi nämä tutkimukset osoittavat oikeaksi myöskin sen aikaisemman olettamuksemme, että tietyt kontaktiäänet eli ns. sosiaaliset äänet saattavat nekin olla vaikeasti paikallistettavia ja näin ollen ovat vihollisen kuultaviksi enemmän tai vähemmän verhottuja, samalla kun ne toimivat esim. parvea koossa pitävinä kutsuääninä. Tällaisina ne myöskin — kuten esim. tiaisilla — saavat aikaan sekaparvien syntymisen, koska niihin sisältyy korkeasävelisiä äänielementtejä, jotka ovat eri lajeilla yhteisiä ja joita nämä siis «ymmärtävät». Lintujen kutsu- ja varotusäänet eivät sävelkorkeutensa ja rakenteensa puolesta ole sijoittuneet niin sanoaksemme vain spektrin kumpaankin päähän, vaan niissä on havaittavissa asteittainen sarja suhteellisen helposti paikallistettavista erittäin vaikeasti paikallistettaviin ääniin.

Muuttolintujen saapuminen Rovaniemelle vv. 1947-1961

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Suomen pitkänomainen ja lintujen muuttosuunnan mukainen asema suo hyvän tilaisuuden tarkkailla muuton vaiheita maamme rajojen sisällä. Kevätmuuton aika ja muuton kehitys tunnetaankin pääpiirteissään jo varsin hyvin, mutta suurimmaksi osaksi vain Etelä-Suomessa tehtyjen havaintojen valossa. Pohjois-Suomessa, käsiteltävänä olevassa tapauksessa Rovaniemellä, suoritettut havainnot osoittavat kuitenkin kevätmuuttoon ja sen kehitykseen liittyvän siinä määrin mielenkiintoisia erikoispiirteitä, että niihin on syytä kiinnittää enemmänkin huomiota.

Havaintoaineisto ja -menetelmät

Rovaniemeä koskevat muuttohavainnot ovat vuosilta 1947—1961 ja niitä koottaessa on käytetty kirjoittajan havaintojen lisäksi rovaniemeläisten lintuharrastajien Juhani Alapullin,