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ON THE ECOLOGY OF HOME RANGE IN BIRDS

Antonio ROLANDO¹

RÉSUMÉ

Un tissu complexe de relations fonctionnelles et hiérarchiques sous-tend l'écologie du domaine vital chez les oiseaux : les patrons spatiaux locaux sont déterminés par des processus écologiques et biologiques qui sont eux-mêmes directement ou indirectement soumis à divers facteurs. Dans cet article, nous examinons ces relations en considérant les déplacements et l'utilisation de l'habitat dans les domaines vitaux. Sur la base d'une analyse critique des données de la littérature, ont été identifiés quatre processus (sélection de l'habitat, reproduction, appariement et grégarisme) et onze facteurs (disponibilité de la nourriture, structure de l'habitat, fragmentation de l'habitat, interactions prédateurs-proies, topographie, effet des activités humaines, conditions climatiques, disponibilités des sites de nidification, âge, sexe et statut social). Les facteurs ont été classés en directs quand ils influencent directement les processus, en indirects quand ils affectent d'autres facteurs qui jouent à leur tour sur les processus, et enfin en faux facteurs quand ils semblent affecter un processus mais qu'en réalité ce sont d'autres facteurs qui agissent. Des considérations quantitatives et ontologiques suggèrent que le processus le plus important dans l'expression des patrons de distribution des oiseaux serait la sélection de l'habitat, elle-même affectée par les disponibilités et la localisation des sources de nourriture. Le principal résultat de cette étude est donc que les disponibilités alimentaires constitueraient le déterminant écologique majeur des domaines vitaux chez les oiseaux, les autres facteurs apparaissant secondaires.

SUMMARY

A complex web of functional and hierarchical relationships underlies the ecology of home range in birds: local spatial patterns are determined by ecological and biological processes which are affected by several factors in a direct or indirect way. This paper deals with these relationships by considering both movements and habitat use within home ranges. On the basis of a critical analysis of factors found in the literature, four processes (*i.e.* habitat selection, breeding, mating and flocking) and eleven true factors (*i.e.* food availability, habitat structure, habitat fragmentation, predator-prey interactions, topography, human disturbance, climatic conditions, nesting site availability, age, sex and social status) have been identified. Factors have been classed as direct in the sense that they directly influence processes, indirect when they affect other factors which then affect processes or false in the sense that they seem to affect processes while, in reality, other factors do so. Quantitative and ontological considerations suggest that the most important process affecting the spatial patterns of birds is habitat selection; it in turn is mostly affected and controlled by food availability and location. Hence, the main result of this study is that food availability is the primary determinant of home range ecology in birds and all the other factors are secondary.

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INTRODUCTION

The study of local movements and spacing of animals can be addressed by considering two major spatial systems, *i.e.* home ranges and territories.

The home range may be defined as “that area traversed by the individual in its normal activities of food gathering, mating and caring for young” (Burt, 1943). It should be underlined that home range is not *all* the area an animal traverses, but rather the area in which it normally moves; accordingly, occasional excursions outside its normal area should not be considered as part of the home range (White & Garrott, 1990). The home range concept has been developing together with radio-telemetric studies focused on local movements and habitat use. When a home range size is estimated, the measured size increases very rapidly when fix-recording starts but as more and more positions are recorded, a point of “sampling saturation” is reached. It is generally assumed that beyond this point the animal’s range does not significantly increase. Home ranges of erratic individuals or floaters are obviously expected to go on increasing, but the presence of a true home range for these individuals can be questioned. However, since many studies have shown continuous range size increases even in apparently sedentary animals, the idea of a stable home range has recently been challenged (Gautestad & Mysterud, 1995).

A territory may be defined as “a more or less exclusive area defended by an individual or group” (Davies & Houston, 1984). However, it is often very difficult to ascertain the exclusive use of an area and to detect the keeping-out signals displayed. Moreover, the same species may be territorial in certain ecological contexts and non-territorial in others (Brown, 1988; Grahn, 1990; Rolando *et al.*, 1995). The degree of overlap between adjacent territories is also variable and the very concept of territorial exclusiveness is far from adequate. Accordingly, the borderline between these two spatial systems is not as clear-cut as may appear from the above-mentioned definitions.

The home range concept is used in a more general and comprehensive way than that of territory. In fact, spatial systems whose exclusiveness have not been ascertained are usually referred to as home ranges, even though they may really be territories. Home ranges are highly diversified, *i.e.* individuals may inhabit areas of different size, use certain portions of their area more often than others (*i.e.* core-areas), frequent two or more distinct and separated areas (*i.e.* disjointed ranges) and overlap to different degrees in the use of the same area (home range overlap).

Birds are highly mobile vertebrates whose home ranges have been studied by radio-telemetric techniques for more than two decades. The way birds use the habitat within their home range has also been extensively studied. Hence, it is nowadays possible to depict a general, comprehensive, *ecology of home range in birds* by considering both habitat use and home range spatial patterns. From this point of view, it is important not to mix *ecological and biological process* with the *spatial patterns* they generate (*i.e.* home range size, core areas, home range overlap, movements, etc.). The topic of habitat selection is central in bird ecology. At a local level, all decisions taken by individuals to better use their habitat fall into the habitat selection process (Cody, 1985). Habitat selection decisions may significantly influence individual movements and spatial distribution and thus it can be assumed that habitat selection is an important ecological process determining the spatial patterns of birds. However, home range spatial patterns may also be

controlled by processes that are independent of habitat selection. For instance, the presence of certain mating systems may significantly influence bird movements, in which case the spatial patterns are controlled by the process of mating.

There are a lot of factors affecting such processes. Many of them are *direct* in the sense that they directly influence the processes of home range ecology (e.g. food availability directly affects habitat selection which affects movements). Others are *indirect* because they affect other factors which then affect the processes (e.g. human disturbance may change food availability which then affects movements) or *false* in the sense that they seem to affect processes while, in reality, other factors do so (habitat type and structure seems to affect birds' decisions whereas the birds might not choose the habitat for its type or structure but rather for its food resources). Since the most impelling need of animals is feeding, food availability (among the different factors) is expected to be an important determinant of home range ecology in birds.

The present paper reviews studies primarily regarding home ranges. The main aims are: 1) to identify ecological and biological processes responsible for the observed spatial patterns; 2) to distinguish direct factors from indirect and false ones, and 3) to weight the factors in order to identify and separate primary determinants of home range ecology from secondary ones.

METHODS

This review considers factors affecting home range in birds. However, in some papers there was no clear distinction between home range and territory, so that spacing systems addressed as home ranges may instead have been territories (especially during the reproductive period). Hence, some of the conclusions drawn here concerning home range ecology may be partly valid for territory ecology as well.

The bibliographical research was carried out by considering papers published from 1980 onwards primarily in indexed journals. For radio-telemetric studies, sample size was carefully considered and studies based on less than ten individuals were, as a rule, excluded. Home range estimates are affected by measurement methods, but this is not influential when quantitative comparisons between different papers are avoided. Twelve main types of factors (or classes of factors) were preliminarily identified on the basis of the results presented in the reviewed papers (e.g. food availability, habitat type and structure, habitat fragmentation, population density, predator-prey interactions, human disturbance, topography, breeding, sex, age, social status and flocking). They were critically analysed by means of a quantitative and ontological approach. Statistics concerning the number of published papers may be questionable since certain topics are investigated more than others (because they are easier to study or because they are "trendy") and positive results are more readily published than negative ones. Nevertheless, the quantification of evidence for the influence of a given factor on home range ecology, based on the proportion of papers that show this influence among those that have investigated it, may be useful, at least to point out general trends. The evidence supporting each factor was quantified by counting the number of papers that ascertained or suggested its influence on local movements of birds. Each factor was examined to make clear if it was a direct, indirect or false factor. In a few instances the analysis made clear that a factor did not affect any process because it was instead a process.

In the present review the term ranging behaviour is used generically to indicate all the movements within individual home ranges. The term spacing is used with regard to territoriality only, and refers to the fact that territorial birds are usually well spaced.

THE FACTORS PRELIMINARILY IDENTIFIED IN THE LITERATURE

FOOD AVAILABILITY

It is well known that food availability may affect the way birds use the habitat within their home range. On average, habitat preferences simply and directly reflect resource abundance, *i.e.* birds positively select those habitats where food is more abundant (or seasonally available). Evidence for this comes from raptors (Kenward, 1982; Brown, 1988; Coleman & Fraser, 1989; Warketin & Oliphant, 1990; Heredia *et al.*, 1991; Beauvais *et al.*, 1992; Carey *et al.*, 1992; Hunt *et al.*, 1992; Génot & Wilhelm, 1993; Laidig & Dobkin, 1995; Austin *et al.*, 1996; Haney, 1997; Plumpton & Andersen, 1997; Linkhart *et al.*, 1998; Tornberg & Colpaert 2001), Galliformes (Wiseman & Lewis, 1981; Smith *et al.*, 1982; Warner, 1984; Erikstad, 1985; Ricci, 1985; Birkan & Serre, 1988; Zwank *et al.*, 1988; Ellison *et al.*, 1989; Storch, 1993a; 1994; Dixon *et al.*, 1996), woodpeckers (Olsson *et al.*, 1992; Doster & James, 1998; Rolstad *et al.*, 1998), Anseriformes (Talent *et al.*, 1982; Spindler & Hall, 1991; Giroux & Patterson, 1995), passerines (Greg-Smith & Wilson, 1984; Patterson *et al.*, 1991; Everding & Montgomerie, 2000); the Lapwing *Vanellus vanellus* (Johansson & Blomqvist, 1996) and the American Woodcock *Scolopax minor* (Hudgins *et al.*, 1985).

Local movements, involved in food finding, are aimed primarily at satisfying individual energy requirements (Mace & Harvey, 1983); hence, the availability of food resources, particularly their abundance and distribution, may significantly control ranging behaviour. When food is abundant, there is no need to increase movements, whereas when food is scarce, individuals are forced to increase movements to find new food resources. Many studies have shown that home range size increases in response to declining resource abundance. This inverse relationship has been described especially for diurnal birds of prey (Marquiss & Newton, 1981; Kenward, 1982; Village, 1982; Griffin & Baskett, 1985; Baker-Gabb, 1986; Robertson & Boshoff, 1986; Brown, 1988; Beauvais *et al.*, 1992; Sodhi, 1993; Babcock, 1995; Whitelaw, 1995; Marzluff *et al.*, 1997), but it has also been found in nocturnal birds of prey (Zabel *et al.*, 1995; Bingham & Noon, 1997), Galliformes (Porter *et al.*, 1980; Connelly *et al.*, 1983; Warner, 1984; Erikstad, 1985; Storch, 1993a), Anseriformes (Talent *et al.*, 1982; Spindler & Hall, 1991; Giroux & Patterson, 1995), Piciformes (Rolstad & Rolstad, 2000), Passerines (Smith & Shugart, 1987; Catterall *et al.*, 1989; Davies *et al.*, 1995; Seki & Takano, 1998), Turnstone *Arenaria interpres* (Metcalf, 1986), Ground Parrot *Pezoporus wallicus* (McFarland, 1991) and the cuckoo *Cuculus canorus* (Nakamura & Miyazawa, 1997). In keeping with these observations, experimental food supply caused a home range restriction in both Dunnock *Prunella modularis* (Davies & Lundberg, 1984) and White-throated Sparrow *Zonotrichia albicollis* (Piper & Wiley, 1990). However, artificial spots of increased prey abundance did not lead to any significant change in home range size in the Great horned Owl *Bubo virginianus*, which simply reacted by visiting these spots more frequently (Rohner & Krebs, 1998).

Home range size may also depend upon the distribution of food, so that the more scattered the resources, the larger the range size. This has been found in some raptors looking for the carcasses of prey (Griffin & Baskett, 1985; Baker-Gabb, 1986; Robertson & Boshoff, 1986).

Also, when feeding resources are clumped in certain sites, the use of home range may be inhomogeneous. For instance, the Great Tit *Parus major* concentrated its activity over these sites (East & Hofer, 1986) and the West Indian Whistling Duck *Dendrocygna arborea* intensively used the areas where food (grain seeds) was artificially supplied (Status, 1998). Boreal Owls *Aegolius funereus* in the northern Rocky Mountains used large home ranges because of the wide geographic dispersion of suitable nesting, roosting and foraging sites (Hayward *et al.*, 1993). Home ranges of the Cuckoo were disjointed when the area selected for reproduction did not provide enough caterpillars, which had to be caught in another area (Nakamura & Miyazawa, 1997). Food distribution and availability may change from season to season and birds may change habitat selection and/or home range size accordingly (Wiseman & Lewis, 1981; Smith *et al.*, 1982; Connelly & Markham, 1983; Zwank *et al.*, 1988; Patterson *et al.*, 1991; Storch, 1993a; Rolstad & Rolstad, 1995; Rolando, 1996; 1998; Rolando & Carisio, 1999).

All the above suggests that, in general, food availability and distribution directly affects the way birds use their habitat and, consequently, the space within their home ranges. Given the above-mentioned evidence and the fact that birds move primarily to find food and satisfy their energy requirements, there is no doubt that food availability is a very important ultimate factor affecting home range ecology in birds.

HABITAT TYPE AND STRUCTURE

Bird species are obviously tied to particular habitat types, selected on the basis of the different vegetation types (grassland, woodland, etc.). Within each habitat type, birds may further select particular habitat sub-types, *e.g.* many forest species have a predilection for peculiar mixed formations (Young *et al.*, 1991; Zwank *et al.*, 1994; Laiding & Dobkin, 1995; Rolando, 1998; Rolando & Carisio, 1999). Habitat structure, *i.e.* the physical characteristics of a habitat type, is also known to affect the habitat selection of birds. They may choose to establish their home ranges in areas with a peculiar habitat structure or select the habitats with a particular structure within their home ranges. Structural characteristics of the habitat include: tree density, canopy and grass cover, tree or grass height, leafage size, trunk diameter and forest age (this factor being tied to several other structural traits), and the presence of perching structures (Porter & Labisky, 1986; Wigley *et al.*, 1986; De Lotelle *et al.*, 1987; Bidwell *et al.*, 1989; Ganey & Balda, 1989; Thompson & Fritzell, 1989; Carey *et al.*, 1990; Stromberg, 1990; Call *et al.*, 1992; Carey *et al.*, 1992; Olsson *et al.*, 1992; Belthoff *et al.*, 1993; Bloom *et al.*, 1993; Storch, 1993a; 1994; Zwank *et al.*, 1994; Fernandez & Azkona, 1996; Perez *et al.*, 1996; Engstrom & Sanders, 1997; Haney, 1997; Kinoshita, 1997; Doster & James, 1998; Haggerty, 1998; Scott *et al.*, 1998; Tornberg & Colpaert, 2001).

The choice of a certain habitat within the home range may also depend on *climatic conditions*. For instance, the Ground Parrot *Pezoporus wallicus* selected different forest areas throughout the year according to the local seasonal degree of

humidity (McFarland, 1991) and Cabot's Tragopan *Tragopan caboti* selected forest zones with a high density of small trunks because they worked as heat-insulators (Young *et al.*, 1991). *Availability of nesting sites* is another key factor controlling habitat selection (Berger & Marchendau, 1988, Olsson *et al.*, 1992; Zwank *et al.*, 1994; Laidig & Dobkin, 1995; Haney, 1997; Mazur, 1998; Scott *et al.*, 1998).

According to many studies, the higher is the proportion of positively selected habitat in the home range, the smaller is its size (Renken & Wiggers, 1989; Carey *et al.*, 1990; Belthoff *et al.*, 1993; Bloom *et al.*, 1993; Storch, 1993a; Zwank *et al.*, 1994; Engstrom & Sanders, 1997; Haggerty, 1998; Scott *et al.*, 1998). However, a few cases where home range size was positively correlated with the amount of preferred habitat have also been reported (Wigley *et al.*, 1986; Ganey & Balda, 1989).

Food abundance and the need to eat or avoid being eaten are also clearly connected with the selection of certain habitat characteristics (see factors 1 and 3, respectively).

All the above suggests that habitat type and structure may affect the habitat selection process, which in turn may affect spatial patterns by determining changes in home range size and structure. However, habitat type and structure is often a false factor. Indeed, in many instances, birds do not select a vegetation type or a certain habitat structure *per se*, but rather select the habitat for the availability of food and nesting resources, or shelter from predators, or climatic conditions.

PREDATOR-PREY INTERACTIONS

It is well known that predators and prey affect each other's habitat selection decisions.

Predators may select habitats where prey are more visible or more vulnerable (Brandl *et al.*, 1986; Hunt *et al.*, 1992; Squires *et al.*, 1993; Babcock, 1995; Austin *et al.*, 1996; Johansson & Blomqvist, 1996; Haney, 1997; Linkhart *et al.*, 1998). Predators may also select the habitats where they are able to hunt (Thiollay, 1991) and avoid ill-suited habitats even though prey are more abundant there (Michelat & Giraudoux, 1993; Austin *et al.*, 1996). Sit-and-wait predators, for instance, are forced to select only those habitats which offer appropriate perching structures (Smith & Gilbert, 1984; Carey *et al.*, 1992; Perez *et al.*, 1996; Kinoshita, 1997).

Conversely, prey may choose habitats which offer effective protection from predators (Kirby *et al.*, 1985, Holbrook *et al.*, 1987; Young *et al.*, 1991; Ellison *et al.*, 1989; Wiseman & Lewis, 1981; Ricci, 1985; Church, 1994; Storch, 1994; Dixon *et al.*, 1996; Scott *et al.*, 1998); accordingly, the seasonal availability of habitats offering protection from predators significantly influences a prey's movement and home range size (Whiteside & Guthery, 1983; Gatti *et al.*, 1989; Taylor & Guthery, 1980). Certain habitats that are positively selected because of their potential protection from predators may be extremely dangerous for prey because they are often visited by predators. This is the case of the pheasant hens which took cover in hedges where foxes hunted efficaciously (Schmitz & Clark, 1999). Conversely, anti-predator behaviour may lead the predator to abandon a certain area where they prey have become too difficult to catch. Young Spanish Imperial Eagles *Aquila adalberti* were found to have temporary home ranges; they settled in an area until the decrease of their success in hunting rabbits (due to the effectiveness of the rabbits' anti-predator behaviour) forced them to leave (Ferrer, 1993).

In summary, predators may directly affect the habitat selection and, consequently, spatial distribution of their prey. From this point of view, predator-prey interactions can properly be considered a direct determinant of home range ecology of prey. This factor may also be a false factor. Prey are the food of predators and thus food availability must be considered as the ultimate determinant of habitat selection of predators. In other instances, predators select habitats where they are able to hunt, *i.e.* they depend directly on habitat type and structure.

HABITAT FRAGMENTATION

The definition of home range in fragmented habitats may be problematic. When the habitat is fragmented, individuals may not use most of the habitat they move into. Thus the definition of home range given in the introduction may not apply. However, it must also be considered that, in many instances, the habitat of inter-fragment areas may still be used by birds. Hence, the fact that in most of the studies concerning habitat fragmentation home range contours encompassed both fragments and inter-fragment areas, may be correct. From this point of view, habitat fragmentation, either natural or human-induced, may cause home range enlargement in species which are strictly dependent on the habitat that has been fragmented or, conversely, may result in a home range reduction in species that use heterogeneous habitats. In the former case, species are forced to move from one fragment to another and thus face the problem of crossing areas of inhospitable habitat. Gap-crossing capabilities vary a lot from species to species and, as a rule, are superior in large-size species (Grubb & Doherty, 1999). Accordingly, small specialised species would be more vulnerable to habitat fragmentation than large ones.

Home range enlargement induced by habitat fragmentation has been found in Strigiformes and Galliformes (Warner, 1984; Gjerde & Wegge, 1989; Carey *et al.*, 1992; Lehmkuhl & Raphael, 1993; Storch, 1993b; Redpath, 1995; Scott *et al.*, 1998). In the Jay *Garrulus glandarius*, home range size was also positively correlated with habitat heterogeneity; in this case, however, the result was explained by assuming that Jays in a heterogeneous habitat take advantage of the heterogeneity. In fact, in the Maremma Natural Park (central Italy), birds visited fragments of different habitat types to forage during the day and came back to the maquis (the original local habitat type) at night (Rolando *et al.*, 1995).

Habitat fragmentation may also cause a change in habitat use. On the island of Java, forest fragmentation induced several raptor species to use sub-optimal habitats. However, this shift was positive and important for bird conservation because it made these species less prone to local extinction (Thiollay & Meyburg, 1988). Habitat fragmentation may be an indirect factor. In the Northern Spotted Owl and in the Jay, fragmentation caused a change in food abundance and distribution, which in turn influenced habitat selection which induced range enlargement; in these cases, food abundance and distribution is the true direct determinant of the birds' movements. Similarly, a study of the movements of the Goshawk in Finland (which, however, failed to show any significant correlation between fragmentation and range size) suggested that forest fragmentation reduced the density of grouse and squirrels, the main prey of male hawks, but possibly increased the number of hares, the preferred prey of female hawks (Tornberg & Colpaert, 2001).

POPULATION DENSITY

Ranging behaviour may depend upon the presence of conspecifics. This is particularly true in territorial systems where there is a functional cause-and-effect relationship between density and territory size, *i.e.* the size decreases with increasing population density. Such a relationship has also been shown for home ranges of several species (Village, 1982; Berger & Marchandea, 1988; Smith & Van Buskirk, 1988; Catterall *et al.*, 1989; Grahn, 1990; Belthoff *et al.*, 1993).

Ranging behaviour may be affected even though there are no differences in home range size. In the Corncrake *Crex crex*, movements within home ranges became more random when population density increased (Grabovsky, 1993). Similarly, the territories of Great Reed Warblers *Acrocephalus arundinaceus* located between two adjacent territories showed two activity centres because males defended both territorial boundaries; in contrast, the territories adjacent to only one other territory showed one activity centre (Rolando & Palestini, 1991).

Densities may depend upon resource abundance, *i.e.* densities increase with increased food abundance and availability. This was demonstrated in the Black-capped Chickadee *Parus atricapillus* by means of artificial extra-food supply (Smith & Van Buskirk, 1988). The very high Jay densities observed in a coastal area in the Maremma Park were explained by the remarkably high abundance of resources that were locally available during summer (Patterson *et al.*, 1991).

Population density does not influence space use *per se* because it is an indirect factor. A high population density may determine a high level of intraspecific competition, which can be considered the true direct determinant of spacing in territorial systems. In fact, a close examination of the reviewed papers suggested that the home ranges described in them were (or might have been) territories. From this point of view, it is probably incorrect to consider intraspecific competition as a factor affecting the home range ecology of birds. However, population density may reflect food availability and, at least in one instance, it was demonstrated that food abundance and distribution was the true direct determinant of home range spatial patterns.

TOPOGRAPHY

Landscape ecology suggests that the spatial structure of the landscape may significantly affect biological processes (Farina, 1998). Therefore, one can expect that habitat selection may be affected and, consequently, home range spatial patterns. There are very few studies of home ranges and topographical factors in birds. Alpine Capercaillies *Tetrao urogallus* preferred gentle slopes independently of habitat structure (Storch, 1993b). In a study area in Arkansas, home range sizes of Red-cockaded Woodpeckers *Picoides borealis* were smaller than in other areas, probably because of the ridged topography of local mountains (Doster & James, 1998). In the Spotted Owl *Strix occidentalis lucida*, the topography did not directly constrain home range size, but it influenced the location of activity centres (Ganey & Balda, 1989).

An analysis of the ranging behaviour of the Alpine Chough *Pyrrhocorax graculus* suggested that the presence of high mountain ridges and the extent of the area available to the birds significantly affected summer movements and home range size: the larger the valley extension, the larger the home range size. In this case, however, movements would also be affected by food distribution (Rolando *et al.*, 2000).

When orographic features are concerned, it may be assumed that topography directly affects the habitat selection decisions of birds, due to the energy costs associated with steep slopes; as a consequence, it may also affect individual movements and spatial patterns.

HUMAN DISTURBANCE

It is generally assumed that human activities and development are detrimental to the ranging behaviour of birds. However, some studies have shown that certain species can indirectly benefit. The Bald Eagle *Haliaeetus leucocephalus* took advantage of both wildfowl hunted as game animals and the construction of hydro-electric power plants. In the former case, fowls took cover in the natural reserve inhabited by eagles which, having more prey, reduced their home-range sizes; in the latter case, fishes were disturbed by the power plant, becoming more vulnerable and more easily caught by the eagles (Griffin & Baskett, 1985; Hunt *et al.*, 1992; respectively). The marsh harrier *Circus aeruginosus* took advantage of the large number of small mammal carcasses along high-traffic roads and, since carcasses were scattered, they enlarged their home-ranges (Baker-Gabb, 1986).

The negative consequences of human disturbance are also numerous. Changes from traditional to intensive farming are associated with home range expansions (Warner, 1984; Kobuek & Kubista, 1990; Tella *et al.*, 1998) and the same is true for disturbed areas where the continuous presence of people, hunting pressure or livestock drive birds away (Connelly & Markham, 1983; Ayeni, 1984; Houard & Mure, 1987; Schultz & Guthery, 1987; Miquet, 1988; Dixon *et al.*, 1996). Disturbed birds may also move for longer distances or spend more time in flight (Zemba *et al.*, 1989; Summers & Critchley, 1990; Clugston *et al.*, 1994; Giroux & Patterson, 1995). The use of sodium ammonium nitrate caused an effective reduction of invertebrates and, consequently, Loggerhead Shrikes *Lanius ludovicianus* greatly enlarged their home ranges (Yosef & Deyrup, 1998). Severe disturbance, in addition to home range enlargement and core area displacement, may also force individuals to shift their home ranges (Andersen *et al.*, 1990).

In other studies the nature of the effects (beneficial or harmful) are debatable. The Rough-legged Hawk *Buteo lagopus* perched on electric cables and fed on carcasses found along roads: home range size and form were clearly influenced by the occurrence of these human structures (Watson, 1986). Nesting Prairie Falcons *Falco mexicanus* did not show any appreciable change in hunting home ranges near oil wells and related developments (Squires *et al.*, 1993). In the Alps, high-altitude urbanization apparently affected the winter ranging behaviour of the Alpine Chough: in this case, the result was a strong reduction of home range size since the birds spent all day inside the local town feeding on scraps, especially bread (Rolando *et al.*, submitted).

All the above suggests that human disturbance may directly affect habitat selection which consequently affects local spatial patterns. However, disturbance may also be an indirect factor because it may determine changes in food availability and distribution or in habitat structure, which in turn influence habitat selection decisions.

BREEDING

A reduction of movements during the breeding period has been found in many species (Kitagawara, 1982; Bjorklund & Westman, 1986; Haug & Oliphant, 1990;

Smith, 1991; Meretsky & Snyder, 1992; Poonswad & Tsuji, 1994; Mazur *et al.*, 1998; Brothers *et al.*, 1998). This pattern of home range size reduction may easily be explained by the need of parents to remain close to the nest. However, a reverse pattern of home range enlargement has been observed in the Australian Brush-turkey *Alectura lathami* (Jones, 1990). It must be considered that Megapodidae do not provide direct parental care; in this case, females moved regularly from one incubation mound to another, thus enlarging their home ranges (Jones, 1990). In penguins, home range size is directly proportional to the age of the chicks: the older they are, the farther their parents move from the nest (Adams, 1987; Brown, 1987; Weavers, 1992). In some species the location of core areas changes between the pre-reproductive and reproductive period, when birds typically concentrate their activities around the nest (Garrett *et al.*, 1993; Marzluff *et al.*, 1997).

During reproduction, ranging behaviour is often sex-related. Brooding individuals, in most cases females, usually show the most dramatic reduction in range size (Marquis & Newton, 1981; Village, 1982; Holbrook *et al.*, 1987; Brown, 1988; Kilbride *et al.*, 1992; Squires *et al.*, 1993; Zwank *et al.*, 1994; Benn & Kemp, 1995; Pnoldmaa & Holder, 1997; Jenkins & Benn, 1998) but individuals defending nest sites (usually males) may reduce their movements as well (Martindale, 1983; Booth, 1987).

The degree of overlap between the home ranges of the male and female of a pair may significantly increase during the breeding period and the female's home range may even be entirely within that of the male (Village, 1982; Belthoff *et al.*, 1993).

All the above clearly demonstrates that breeding constraints certainly and ultimately limit bird movements during reproduction. However, it must be underlined that breeding cannot be considered as an independent factor because it is a process. Hence, it is the *breeding process* that significantly controls spatial patterns in breeding individuals during the reproductive period. This process obviously may be affected by factors such as sex and age.

AGE

In many species the home ranges of adults are significantly smaller than those of juveniles, which are usually floaters and move a lot looking for a site in which to settle down (Kenward *et al.*, 1981; Marquiss & Newton, 1981; Graves *et al.*, 1983; Wegge & Larsen, 1987; Berger & Marchandeu, 1988; Catterall *et al.*, 1989; Gjerde & Wegge, 1989; Gatti *et al.*, 1989; Nesbitt & Williams, 1990; Piper & Wiley, 1990; McFarland, 1991; Storch, 1993b; Shutler & Weatherhead, 1994; Badayev *et al.*, 1996; Warnok & Takekawa, 1996; Rolando & Carisio, 1999). In the Ground Parrot *Pezoporus wallicus*, adults are long-term residents of sites and may occupy the best feeding areas; consequently they have smaller ranges than subadults, which have to move widely using marginal patches (McFarland, 1991).

In other species, however, the relationship is reversed and adults move for longer distances than juveniles (Lindsey *et al.*, 1991; Giroux & Patterson, 1995; Sol & Senar, 1995). In these cases, flocking processes, such as the temporary non-integration of juvenile parrots into adult flocks (Lindsey *et al.*, 1991), may be involved. Finally, in some studies, no significant differences between juveniles and adults have been found (Green, 1983; Griffin & Baskett, 1985; Smith & Van Buskirk, 1988; Clarke & Fitz-Gerald, 1994).

The usual greater mobility of juveniles may easily be explained by assuming that they become familiar with the local environment only by exploring it everywhere. Although age may be a false factor, in most cases age may directly affect the process of habitat selection, which determines the ranging behaviour of birds.

SEX

Males and females may present home ranges of different size: sometimes larger in the male (Berger & Marchandeu, 1988; Ellison *et al.*, 1989; Birkan & Serre, 1988; Storch, 1993a), other times larger in the female (Graves *et al.*, 1983; Gjerde & Wegge, 1989; Solis & Gutierrez, 1990; Perez *et al.*, 1996; Enderson & Craig, 1997; Ziesemer, 1997). Sex differences may depend on several factors. Sex-related home range size may depend on mating systems: in the Alpine Accentor *Prunella collaris*, males had larger ranges than females to gain and monopolize mates; in fact, male ranges encompassed the boundaries of several female ranges (Davies *et al.*, 1995). In the partridge *Perdix perdix*, male-male competition may lead to greater instability of home ranges, which are thus larger than the female ones (Birkan & Serre, 1988). In lek-species, social organization strongly influences spatial patterns: especially during the reproductive period, females usually range more widely than males, which are tied to their leks (Graves *et al.*, 1983; Gjerde & Wegge, 1989).

However, in most studies, range differences between sexes turned out to be non-significant (Porter *et al.*, 1980; Whiteside & Guthery, 1983; Marti, 1985; Brown, 1988; Smith & Van Buskirk, 1988; Jones, 1990; Belthoff *et al.*, 1993; Zwank *et al.*, 1994; Storch, 1995; Nakamura & Miyazawa, 1997; Selas & Rafoss, 1999).

Some investigations also revealed sex differences in habitat selection. In size-dimorphic species, it has been suggested that males and females have distinct predator avoidance strategies and may select different habitats accordingly (Ellison *et al.*, 1989; Storch, 1993a) and/or that the smaller sex is able to utilize denser forests which cannot properly be used by the larger sex (Solis & Gutierrez, 1990; Storch, 1993a). In the Black-throated Blue Warbler, males and females had different diets and selected different habitats (Wunderle, 1995).

All the above suggests that sex may influence at least two different processes. Each sex may have different predator avoidance strategies or use the habitat in different ways and, hence, sex indirectly influences the process of habitat selection. Mating and lek-systems fall into the *mating process* which is, therefore, directly affected by sex.

SOCIAL STATUS

Individual social status, *i.e.* if the bird is single or paired, dominant or subordinate, may significantly influence the ranging behaviour. Home ranges of paired birds are usually smaller than those of unpaired birds (Smith *et al.*, 1982; Birkan & Serre, 1988; Berger & Marchandeu, 1988; Mellen *et al.*, 1992; Meretsky & Snyder, 1992; Bull & Holthausen, 1993; Montadert, 1995; Rohner, 1997).

Home ranges of dominant individuals may be smaller than those of subordinates (Metcalf, 1986; Piper & Wiley, 1990; McFarland, 1991).

According to Grahan *et al.* (1993), dominance in the male pheasant did not significantly influence home range size, although the most attractive males had larger home ranges.

Social status may be an indirect factor. For instance, in the Ground Parrot, dominant individuals had smaller ranges than juveniles because they exploited more productive areas (McFarland, 1991); hence, food availability was the true direct factor affecting habitat selection process. Moreover, unpaired birds are often juveniles and, in this case, age directly affects habitat selection that determines individual spatial patterns.

FLOCKING

The tendency to join into groups may affect home range ecology. In the Black-capped Chickadee *Parus atricapillus*, individuals that were well integrated and stayed in the middle of a flock had smaller home ranges than those that were not integrated and remained at the edge of a flock (Smith & Van Buskirk, 1988). Aggregations of different flocks may also change space use. In the Great Tit *Parus major*, two types of winter flocks have been described. One is the basic flock with constant membership throughout the winter; the other is the compound flock formed by the aggregation of basic flocks. Home ranges of compound flocks are larger than those of basic flocks and this seems to increase the probability that an individual will locate and exploit food effectively (Saitou, 1982).

The classification of flocking as a factor is likely incorrect because it is a behavioural *process* by which birds join into groups to obtain feeding or predator-avoidance advantages.

THE FACTORS AND PROCESSES IDENTIFIED IN THIS STUDY

FACTORS

Most of the reviewed papers ($n = 171$) succeeded in showing that the considered factors affected ecological and biological processes. Studies that failed to show any significant influence of the factor taken into account regarded sex (47.8 % of the 23 papers that investigated sex), age (17.4 % of 23 papers) and social status (8.3 % of 12 papers).

Detailed examination of each of the reviewed papers also allowed me to distinguish direct from indirect and false factors. It should be underlined that all the papers regarding food availability ($n = 75$) concluded that this factor significantly and directly affected home range ecology in birds. Nesting site availability, climatic conditions and topography (at least when the occurrence of steep slopes significantly affected the birds' energy requirements) were other direct factors.

The remaining factors sometimes acted directly, sometimes indirectly, or were false. Some of the papers concerned with habitat type and structure (16 out of 40, *i.e.* 40 %) demonstrated that it was a false factor, since the birds used the habitat because of the food resources, nesting sites or climatic conditions found in

it. Similarly, 53.3 % of the studies dealing with predator-prey interactions (14 out of 30) demonstrated that predators selected habitats where prey were available (thus food availability was the true direct factor) or where they were able to hunt (habitat type and structure). However, the remaining 46.7 % of papers demonstrated that prey selected habitats that offered effective or potential protection from predators, *i.e.* the predators significantly and directly affected the habitat selection of the prey. Habitat fragmentation may work mostly as an indirect factor; 3 papers out of 9 showed that fragmentation induced a change in food availability, so the birds modified their habitat selection processes and consequently their spatial systems. Human disturbance was found to directly affect home range ecology in 81 % of papers (out of 21), while in 19 % of papers, disturbance was an indirect factor because it changed food availability or habitat structure.

Inter-individual differences due to age, sex or social status were only observed in some studies which are considered here to compute proportions. The effects of sex, age and social status may not be easily separated because in many species sex and age determine social status, which affects both the probability and conditions of breeding (see below, processes). Therefore, the suggestions obtained from percentages are weaker than those for other factors; nevertheless, when cautiously considered, they may be useful. In 78.9 % of studies (out of 19), age significantly and directly affected the habitat selection process, and this determined movements. However, in 10.5 % of studies, it was a false factor, since food availability and flocking were directly involved. Sex directly affected sex-related processes in 4 papers out of 12, but 5 studies showed that the direct factors were food availability, predator-prey interactions and habitat structure. As previously pointed out, social status directly and indirectly affected breeding; moreover, in some cases, it may be a false factor. In at least 1 paper out of 11 the direct factor was really food availability; moreover, unpaired birds were often juveniles and age was therefore the working factor.

The other factors preliminarily identified in the literature did not properly fall within the scope of the present review, or were incorrectly classified. Population density is a completely indirect factor since it significantly affects the level of intraspecific competition, the true direct determinant of territoriality. The reviewed papers referred to birds' home ranges, but they were likely territories instead; therefore, intraspecific competition cannot be considered as a factor controlling home range ecology in birds. Finally, breeding and flocking are, in reality, biological processes (see below).

In summary, eleven true factors are identified in the present review: food availability, habitat structure, predator-prey interactions, habitat fragmentation, topography, human disturbance, nesting site availability, climatic conditions, sex, age and social status. Among all these true factors, food availability is the only one that always directly affects home range ecology (the effect of topography, climatic conditions and nesting site availability are likely marginal). The other factors may be direct but in many instances are false or indirect, often because food availability is the only direct factor. Moreover, while many other factors affect only certain species (predators affect the home range ecology only of their prey) or habitats (*e.g.* only fragmented forests) and sometimes do not work at all (*e.g.* age, sex and social status), food availability affects all individuals of all species, everywhere and at all times. All the above clearly suggests that food availability is the most important factor controlling the ecology of home range in birds and that the other factors are secondary.

PROCESSES

Many of the identified factors affect the process of habitat selection. In particular, food availability, habitat type and structure, habitat fragmentation, predator-prey interactions, human disturbance, nesting site availability, climatic conditions, age and sex significantly and directly affect the way birds use their habitat. Moreover, habitat selection may also be indirectly affected. In turn, habitat selection choices affect the way birds move locally. Breeding is another process affecting home range spatial systems of breeding individuals during the reproductive period. It may be affected by the sex, age and social status of the birds. Other processes that may also occasionally affect home range spatial patterns of birds are mating (influenced by sex and age) and flocking.

All these processes are obviously not mutually exclusive since spatial patterns may be contemporaneously determined by more than one factor. For instance, movements of breeding birds may be constrained by the need to defend eggs or nestlings, while at the same time they also depend upon the habitat selection decisions regarding food finding, predator avoidance, etc. From this point of view, it must be stressed that habitat selection is probably more widespread than the other processes. The papers analysed in the present review identified factors that significantly affected processes 249 times (note that several papers identified more than one factor). Most of the time, the identified factors affected, directly or

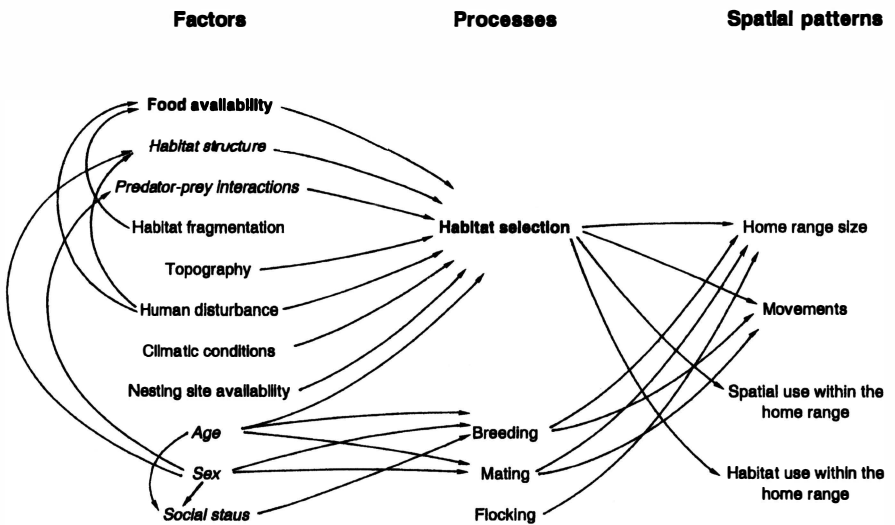


Figure 1. — The complex web of relationships among factors, processes and spatial patterns depicting the ecology of home range in birds. Factors may directly or indirectly affect processes. In the former case the arrow starts from the factor considered (on the right) and hits a certain process, whereas in the latter case the arrow starts from the factor considered (on the left) and hits another factor. Possible false factors are shown in italics. Food availability (among factors) and habitat selection (among processes) are evidenced in bold types because of their importance. Age, sex and social status affect factors and processes in the sense that individuals of different age, sex and social status may behave differently with regard the factor or the process concerned. Spatial use within the home range refers to the presence of disjointed ranges, distinct core areas and various degree of overlap between adjacent home ranges.

indirectly, the habitat selection process (82.3 %). Hence, the overall evidence clearly suggests that habitat selection is the most important process affecting spatial patterns in birds.

CONCLUSIONS

It is now possible to clarify the biological mechanisms underlying home range ecology in birds. Functional relationships among factors, processes and patterns are hierarchical in the sense that home range spatial patterns are determined by ecological and biological processes, which in turn are affected by factors in a direct or indirect way. There are numerous relationships among factors, between factors and processes, and between processes and spatial patterns; these can be represented by a diagram like that of figure 1. This figure shows all the processes (*i.e.* habitat selection, breeding, mating and flocking) and factors (food availability, habitat type and structure, predator-prey interactions, habitat fragmentation, topography, human disturbance, age, sex, social status, nest site availability, and climatic conditions) identified by means of the critical analysis of the literature previously done. Although it is obviously not possible to weigh precisely all the factors and processes to obtain precise hierarchies, this review clearly suggests that the most important process affecting spatial patterns in birds is habitat selection, which in turn is mostly affected and controlled by food availability and location. Hence, the main conclusion is that food availability is the primary determinant of the home range ecology of birds and all the other factors are secondary.

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