Oecologia (1990) 83:68–75

Oecologia

Seasonal variation of territory size with the Little Owl (*Athene noctua*)

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Received November 7 1989 / Accepted December 12, 1989

Summary. In a population of Little Owls (*Athene noctua*) at the Lower Rhine (FRG), the factors were studied that influence the size and shape of territories of this non-migrating, all-year territorial owl species. These studies were carried out between September 1984 and June 1987. The birds were individually marked with transmitter packages so that their locomotional movements could be monitored. Using a standard protable stimulus (a dummy with an attached loudspeaker) the territorial boundaries of 19 male Little Owls were surveilled during the different seasons of the year. Male Little Owls defended their territories in all seasons, but distinct seasonal changes of intraspecific aggressiveness and territory size were observed. The seasonal variations of territory size followed a common pattern in all studied Little Owls, in spite of individual differences in the size of the defended areas. The largest territories were defended in March/April during the courtship season ($\tilde{x}$= 28.1 ha). In May/June all male Little Owls reduced the size of their territories ($\tilde{x}$=12.6 ha). This corresponds to the breeding and nestling period. The yearly minimum of territory size ($\tilde{x}$=1.6 ha) was reached in the summer months July and August when the fledglings were still fed in the parental territory. When the first-year birds started to disperse in autumn (September/October), the size of the defended areas of the adult tenants again increased ($\tilde{x}$=9.5 ha). In winter (November to February), a further increase in territory size was observed for periods of warm weather ($\tilde{x}$=19.8 ha). Male Little Owls, however, were less aggressive during winter than in the following courtship season. On cold winter days with a ground cover of snow territorial aggressiveness ceased. Pastures and meadows offered a continuous food supply almost throughout the year. In some seasons they were overproportionally represented in the territories of Little Owls compared to the general surroundings. In reaction to changing accessibility of food, the hunting ranges within the home ranges were shifted much faster than the boundaries of the defended territories. The significance of various factors contributing to the variability of territory size in Little Owls are discussed (e.g. availability of food, seasonal and individual differences in aggressiveness, experience in the occupied area, population density).

Key words: *Athene noctua* – Territory – Seasonal variation

Territory size is one of the major characteristics of territoriality. Although territorial behaviour has been studied in a number of species, there is still no general agreement about its biological significance. Due to this controversy there also is disagreement about the factors determining the territory size. In this context the discussion centers on the points of seasonal variation of territory size (Ickes and Ficken 1970; Knapton and Krebs 1974; Stefanski 1967), habitat specific and species specific minimum territories (Huxley 1934; Hinde 1956; Klomp 1972; Krebs 1971; Nice 1941; Smith 1974; Tinbergen 1957) and a correlation between population density and territory size (Emlen 1973; Hinde 1956; Krebs 1971; Lack 1954, 1964; Wynne-Edwards 1962). Up to the present most studies have delt with territoriality as a seasonal phenomenon (short-term territoriality). However and particularly in a number of long lived and non-migrating bird species territorial behaviour can occur throughout the year. These birds (e.g. certain birds of prey, owls and corvids) often occupy their once established territory throughout their lives. In addition to the short-term conditions of the habitat and the breeding density during the reproductive season, the territories of these birds are adjusted to long-term influences and effects. Patterson (1980) and MacLean and Seastedt (1979) postulate that species with long-term territories will therefore defend larger areas than they require for their immediate needs. Like Southern (1970) they believe that long-term territories are habitat specific in their size, but are more or less stable in their dimensions over a long period of time (even many years). Kalela (1959), Klomp (1972)

and Newton (1979), on the other hand, observed that the intensity of territorial behaviour in non-migrating territorial birds is also subject to seasonal variations. Kalela therefore postulated that the size of their territories would vary with the seasons. Studies of long-term territoriality in non-migrating birds have so far been carried out with Tawny Owls (Southern 1970), Carrion Crows (Charles 1972; Spray 1978) and Little Owls (Exo 1987). However, seasonal variations of territory size were not the major concern in these studies. The object of the present study on Little Owls was to gain further knowledge about long-term territoriality and the factors influencing it. In particularly the following questions were of interest:

1. Are the intraspecificly defended areas subject to seasonal variations in size?
2. Is territory size and quality influenced by certain habitat structures?
3. How do territories and home ranges of Little Owls correlate?

The definition of territory as "defended area" is widely accepted (Nobel 1939; Hinde 1956; Brown 1969; Wilson 1975) and is used this way in this study. Home ranges are defined as "the area that embraces all the activities of a bird (under natural conditions) during a given time period" (Newton 1979). Little Owls defend territories of type A (food and nesting territories) according to the classification of Nice (1941) and Wilson (1975).

Study area and methods

The study was conducted between September 1984 and July 1987 on the Lower Rhine south of the town of Emmerich, FRG (51°50'N, 6°15'E). Male Little Owls were individually marked with transmitter packages (BIOTRACK SR-1) of distinct frequencies (detailed description in Exo 1987).

Determining home ranges

The home ranges of all studied male Little Owls were regularly determined by means of radio tracking. For this purpose all movements of a Little Owl were continuously monitored during the early night peak of its activity (for about 4–5 h, starting at sunset), this being the time of their most extensive locomotional activity (Exo 1987, 1988). The locations of the Little Owl as determined by radio tracking were supplemented by direct observations through night vision equipment (ZEISS Orion B). A survey of each home range was carried out 4 to 5 times over a two month period. The polygon surrounding all the locations of each of these surveys (maximum polygon) was considered to be the representative home range for this period. As the results of studies by Exo (1987) and myself (Finck 1989) have shown, more frequent observations of Little Owls would not yield extensions of the determined ranges of any considerable size.

Determining territory size

The defended territories of male Little Owls were determined by means of dummy experiments during the early night peak of activity mentioned above. For this purpose territorial calls of Little Owls were replayed from a hide out with a given time pattern and transmitted by a loudspeaker attached to the dummy.

The reactions of the Little Owls were monitored directly by night vision equipment and/or indirectly by radio tracking. These observations were carried out from hide outs at 50 to 200 m distance. The owls' reactions to the experiments were scored according to their level of aggressiveness: (1) acoustic reaction, (2) a directed flight towards the dummy (first approach), (3) an approach within 10 m of the dummy, (4) attack of the dummy. For all these levels of aggressiveness the time of their first appearance in the course of the experiments was recorded, if possible.

Compared with territorial disputes observed under natural conditions, the two highest levels of aggressiveness correspond to the behaviour of territorial tenants towards an actual intruder into their territories. An acoustic reaction and a slight approach towards a potential competitor could also be observed under natural conditions, if a territorial "guhk"-call was uttered outside the boundaries. Therefore the boundaries of the territories were determined as the outermost dummy positions where an approach within 10 m and/or an attack by the territory tenant of the dummy was still to be observed. In the course of the study the sizes of home ranges and territories of 19 different male Little Owls were surveyed over different periods of the year. A total of 45 home range sizes and 36 territory sizes were determined.

Agriculturally utilization of the region observed

The agricultural utilization in the study area was recorded for the different allotments in June of each year. Additionally the portion of the various agricultural areas in the Little Owl territories was determined for each seasonal period.

Statistical tests

The statistical evaluation of the results was carried out with the software package SPSS 9.0 at the Regional Computer Center at Cologne. Further statistical tests and calculations were carried out in accordance with Sachs (1984).

Results

Observation of naturally occurring aggressive behaviour

The arrangement of the dummy experiments had been developed considering preliminary experiments of Exo (1987) and my own observations of naturally occurring territorial disputes. These had shown that spontaneous territorial disputes were regularly triggered off by the intrusion of a male Little Owl into a foreign territory. As soon as the intruder was spotted, the territorial tenant approached and uttered its territorial calls. If the intruder did not retreat, the territorial tenant would fly directly towards it. This normally caused the intruder to flee. In case this first approach was unsuccessful in expelling the intruder from the territory, the tenant would repeat the approach, this time trying to hit the intruder with its claws. To evade injury an attacked owl would let itself drop to the ground, to subsequently flee.

Two events were observed in which the territorial boundaries were obviously disputed between neighbours. In both instances the intruder was attacked while sitting on a pole. The competitors hit each other with beaks and claws while dropping to the ground. Then both retreated with the apparently superior owl staying

in close vicinity and the inferior male fleeing a longer distance.

One important difference between a naturally occurring intrusion into a territory and our dummy experiments was that the dummy sat motionless on its pole. The aggressiveness towards an intruder, however, is enhanced by movements (Amlaner and Stout 1978 on the Glaucous-winged-gull; Shalter 1978 on the Pied Flycatcher). Furthermore the time pattern of the replayed territorial calls was to rigid, although patterns from calls uttered in naturally occurring instances were used. In a natural situation, however, the intruder can react to the territorial tenant by varying the type, frequency and intensity of its calls and other aspects of its behaviour. This might be the reason for the observation that in most cases aggressive behaviour occurred much faster in natural territorial disputes than in the majority of dummy experiments. In dummy experiments a variable reaction towards the territorial tenant can only be simulated with difficulty. On the other hand, no such effort was made in order to guarantee a comparable standard situation in the experiments. Effects of habituation played only a minor role in the experiments, because the number and timing of the experiments were selected in a way to minimize these effects (Finck in prep.).

Seasonal variations in the pattern of reactions towards the dummy

By adding up the monthly results of the dummy experiments it became obvious that, in the course of a year, there are five distinct periods. Between these periods the frequencies of the registered reactions towards the dummy varied considerably (Fig. 1):

All the recorded aggressive behaviours were most pronounced in early spring during the months of March and April. In this period the reaction was faster than in any other time of the year.

In May and June (late spring) the level of aggressiveness of male Little Owls towards the dummy decreased.

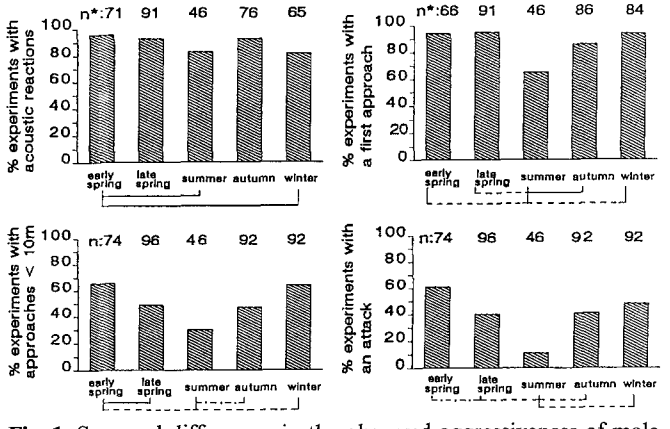

Fig. 1. Seasonal differences in the observed aggressiveness of male Little Owls towards a dummy. The relative frequencies of dummy experiments are shown in which the registered behaviour could be observed. *Not in all experiments a reaction could be clearly registered. (— $p<0.05$, –·–·– $p<0.01$, — $p<0.001$, χ^2-test).

This is shown most obvious by the frequencies of physical attacks upon the dummy. The reaction in these months were somewhat slower.

In summer (July/August) the aggressiveness was significantly reduced. Some males did not attack the dummy at all in these months, but stayed in its direct proximity (10 m) during the experiments.

Beginning in September (autumn) the aggressiveness increased again. Aggressive behaviour was observed in a comparable frequency like in late spring but did not reach the level of early spring. In winter (November to February) only minor changes compared to the aggressive behaviour in autumn were observed. On mild winter days the behaviour of Little Owls closely resembled their behaviour in autumn. Low outdoor temperatures, however, caused the Little Owls to be less aggressive (Finck in prep.). Acoustic reactions, in particular, were significantly slowed down during these months. The aggressiveness of male Little Owls increased once again with the beginning of spring.

To what extent the aggressive behaviour of Little Qwls is subject to variations from year to year on top of the observed seasonal variations cannot be definitely judged from the existing data. Merely the experiments of Exo (1987) which had been conducted in the same area and with a similar method can, with some restrictions, be used for comparison. This suggests that there exist no pronounced yearly differences in the level of aggressiveness of Little Owls.

Variation of home range size and territory size

The study of home ranges and territories of male Little Owls revealed (a) that male Little Owls are territorial all year round and (b) that their home ranges and territories are not necessarily identical in their extensions as suggested by Exo (1987). Even if in some cases home ranges were defended in all their extensions, it was often observed that home ranges and territories differed in size and shape. As will be shown in the following the pattern of seasonal variations differs between home ranges and territories.

Seasonal variation of territory size

In spite of major differences in the determined territory sizes (range: 1–68 ha, $\tilde{x}=12.3$ ha), the size variation within each of the five chosen time periods, namely early spring (March/April), late spring (May/June), summer (July/August), autumn (September/October) and winter (November to February), was much smaller than over the whole year. Furthermore, the seasonal variation of territory size followed a common pattern in all the male Little Owls studied (Fig. 2):

The largest territories were defended in March/April of each year. This is the major courtship season of Little Owls. As mentioned above this is also the time of their most pronounced aggressive behaviour.

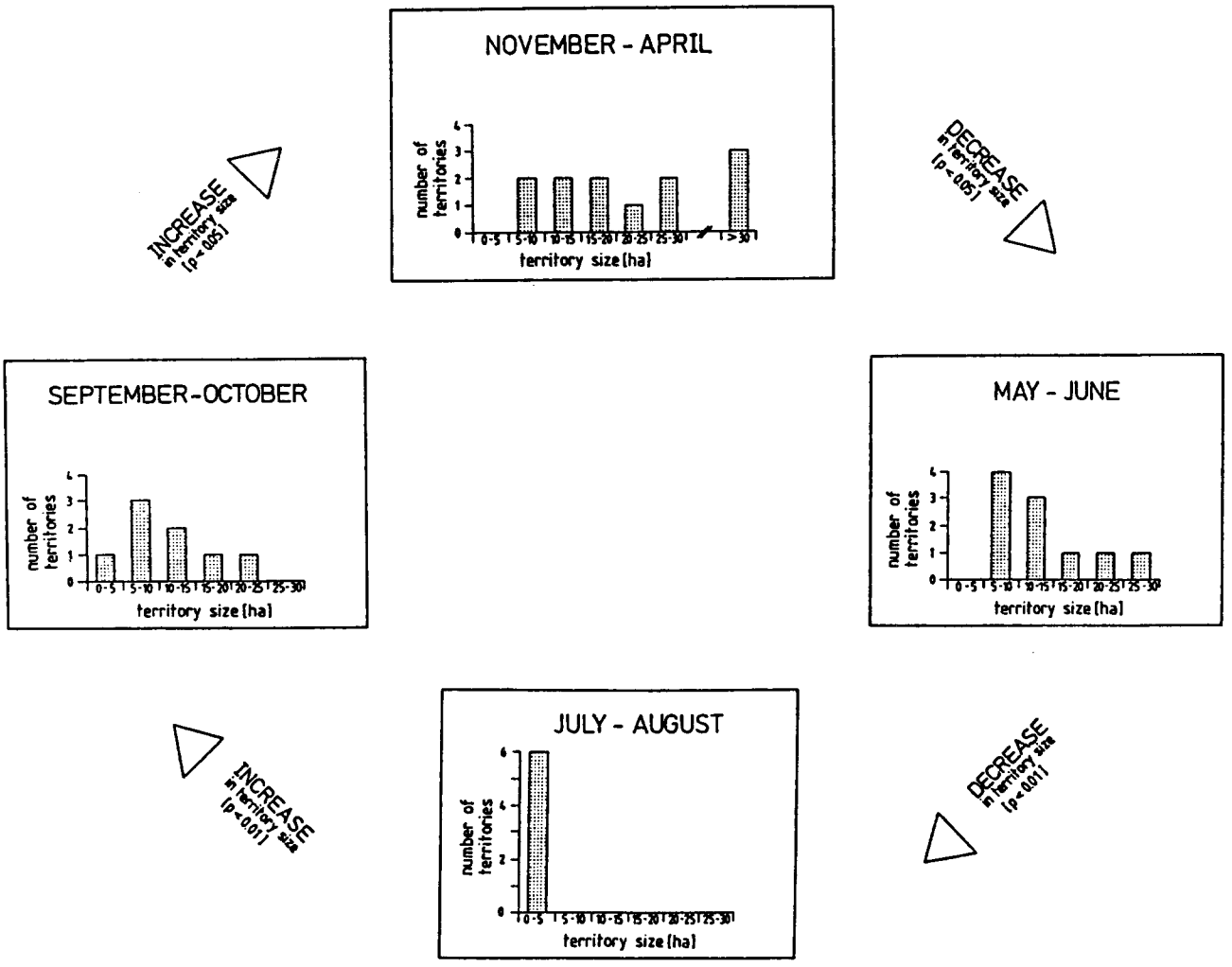

Fig. 2. Seasonal differences of territory size in male Little Owls

In May/June, during the breeding and nestling period, the size of all territories was reduced. The decrease in average territory size from March/April ($\tilde{x}=28.1$ ha) to May/June ($\tilde{x}=12.6$ ha) was significant (Wilcoxon matched pairs signed rank test, $n=6$, $p<0.05$).

Similarly drastic is the observed reduction of territory size towards summer (July/August). In this period of the lowest level of aggressiveness by far the smallest territories in the course of a year were defended. They varied in their size between 1 ha and 4 ha ($\tilde{x}=1.6$ ha). This decrease of territory size was also statistically evaluated (Wilcoxon matched pairs signed rank test, $n=6$, $p<0.05$).

In autumn (September/October), when the first-year birds dispersed, the size of the adult males' territories increased again (Mann-Whitney's U-test, $n=6$, $m=4$, $U=0$, $p<0.01$). Territories of 9.5 ha (median) were defended.

A further enlargement of the territories took place during winter (November–February) (Mann-Whitney's U-test, $n=7$, $m=7$, $U=5$, $p<0.05$). An area of 19.8 ha (median) was defended by Little Owls in these months.

There were only minor differences between the average territory sizes in winter and in early spring. The defended areas in early spring were slightly larger, but this increase could not be evaluated statistically. Therefore the results from these two periods were added together in Fig. 2. However, it should be remembered that the territorial behaviour of Little Owls differs between winter and early spring in that the highest level of aggressiveness is reached during the courtship season (March/April).

The territory size of Little Owls is further influenced by the experience they gained in their territories. Inexperienced males defend larger areas than experienced ones (Finck in prep.). The pattern of seasonal variation of territory size, however, was comparable in all birds, irrespective of their time of experience in the individual territories. Therefore, in this paper no distinction is made between territories of experienced and inexperienced occupants.

Seasonal variation of home ranges

The variation in home range size (range: 2–107 ha, $\tilde{x}=$ 14.6 ha) was larger than the variation in territory size

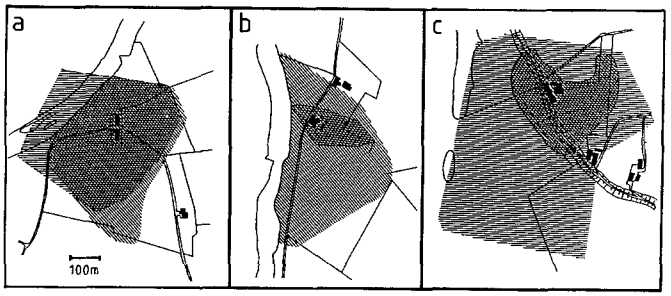

Fig. 3a–c. Home ranges (horizontal shading) and territory size (diagonal shading) of three different male Little Owls from the study area. Time of determination: **a** Sept./Oct. 84, **b** Sept./Oct. 84, **c** May/Jun. 86. Same scale for all figures

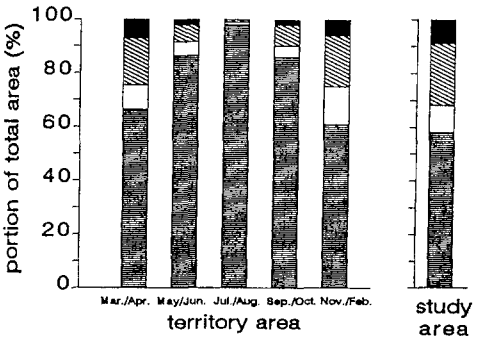

Fig. 4. Seasonal differences in the composition of the areas defended by Little Owls (territory area). The mean portion of four types of agricultural utilizations in the territories are shown. For comparison the portion of these four types of agricultural utilizations in the study area as a whole are given (three year mean) ▤ pastures, meadows; □ corn; ▧ wheat, barley; ■ sugar beets

(range: 1–68 ha, $\tilde{x}=12.3$ ha). Home ranges did not follow the regular seasonal pattern in size of the territory sizes. With the exception of autumn, the sizes of the home ranges, as a rule, were larger than or nearly identical to the corresponding territories (Fig. 3a, c). In autumn, however, the areas defended by Little Owls in the dummy experiments were in some cases considerably larger than the areas they utilized when there was no experimental interference (Fig. 3b). But it has to be kept in mind that only the home ranges of male Little Owls were determined. Since home ranges of males and females can differ (Exo 1987) it is possible that male Little Owls defended the home ranges of their mates in addition to their own home ranges.

Yearly variations of territory and home range sizes

Only slight variations of territory size were observed from year to year during the study. Once, in March/April 1987, the territories were observed to be considerably larger than in earlier years. This was most probably due to the fact that two of the three territories surveilled in this period had just recently been occupied by males. Further information about the importance of knowledge of terrain to territory size is presented elsewhere (Finck in prep.).

A comparison of home range sizes over the years, on the contrary, revealed significant differences particularly when comparing the time period from May to June (August) in these years. In spring 1986 home ranges were considerably larger ($\tilde{x}=44.6$ ha) than in the same period in 1985 ($\tilde{x}=8.7$ ha, $p<0.01$, U-test). Home ranges established in spring 1987 were again smaller than in 1986. Since for these years no data were available on the population density of food animals in the study area, one can only speculate about the reasons for the observed differences in home range size.

The influence of agricultural utilization on size and shape of territories

In establishing the borders of Little Owls' territories for the different seasons of the year, it became obvious that the shape, and possibly also the size, of the defended areas were correlated to the agricultural utilization of the various allotments in the area. In respect to the seasonal development of vegetation cover and vegetation height in the study area, four types of agricultural utilizations could be distinguished: (1) Pastures and meadows offer easy access to food for Little Owls almost throughout the year. This is due to the relatively low vegetation height in these areas. (2) Barley fields are unsuitable for hunting from early-May to mid-July, wheat fields from mid-May to mid-August. This is caused by excessive vegetation height in these periods. (3) Corn fields cannot be utilized by Little Owls for hunting between July and September/October. This is also caused by the vegetation height in that period. (4) Sugar beet fields develop a very dense vegetation cover from September on. As a consequence they cannot be used by Little Owls for hunting until November.

Particularly during the summer half-year which represents most of the vegetation period for the cultivated plants in the study area, the portion of arable allotments in Little Owl territories did not correspond to their portion in the study area as a whole (Fig. 4). Especially in July and August, when Little Owls have the smallest territories in the course of a year, the main areas defended were meadows and pastures. Sometimes the boundaries of meadows and pastures (e.g. fences, ditches, roads) actually correspond to the territorial borders of the Little Owls. Thus, in this period, territories were reduced concentrating the defended areas on allotments that still guaranteed optimal accessibility of food. In this context it is interesting to note that the discrimination of arable lands by Little Owls did not correspond directly to the birds' potential accessibility of these allotments. Thus, the areal portion of corn and sugar-beet fields in the territories was reduced already some time before these areas could not be used anymore for hunting due to vegetation height or dense cover, respectively. Barley and wheat fields, on the other hand, amounted to only a small portion in Little Owl territories even in September/October, although by then they

were easily accessible for the birds due to the harvest in July and August, respectively.

Comparing defended areas with areas utilized for hunting

Comparing the areal portions of the various agriculturally utilized allotments in the territories and their utilization for hunting by Little Owls, some interesting facts were revealed: As mentioned above, corn and sugar-beet fields were only defended to a small extent in late spring (May/June). In these months, however, their portion relative to the home ranges of Little Owls was almost equal to the portion of these areas in the study area as a whole. This was particularly so for sugar-beet fields. Furthermore, it was observed that some Little Owls still performed aggressive behaviour towards the dummy in barley and wheat fields with an actual vegetation height of even 80 cm. In this state these areas could certainly not be used by Little Owls for hunting. On the other hand Little Owls visited certain allotments immediately after harvest for hunting; on these allotments no aggressive behaviour occurred initially towards a dummy subsequently posted there. It was observed, however, that in all seasons more than 90% of the area defended by Little Owls is suitable for hunting with regard to the actual vegetation structure.

Discussion

Territorial behaviour is a type of aggressive behaviour attached to a certain area (Tinbergen 1957; Stephan 1976). Due to this attachment it can be studied with dummy experiments. Furthermore, the extension of the area in which this behaviour is performed can be experimentally established (Cade 1955 on American Kestrels; Cave 1968 on Kestrels; Dhondt and Schillemanns 1983 on Great Tits; Falls 1981 on song birds; Melemis and Falls 1982 on White-throated Sparrows; Nero and Emlen 1951 on Red-winged Blackbirds; Spray 1978 on Carrion Crows). In some species, the boundaries of these defended areas are well defined (Exo 1987; Nero and Emlen 1951); contrary to the suggestion by Kaufmann (1983) boundaries are not arbitrarily abstracted by the observer. The territories of Little Owls studied here in fact had accurate borders. In many cases the locations in which the dummies were attacked by neighbouring males were less than 3 m apart.

Some biotope structures can influence both size and shape of the territories due to their significance regarding nourishment and reproduction (Armstrong 1965; Boxall and Lein 1982; Kenward 1982; Klomp 1972; Southern 1970). This is particularly true for organisms that defend nest and food territories. It is manifested by the observations that distinct biotopes or landscape elements are overproportionally represented in the territories relative to the general surroundings (Boxall and Lein 1982; Kenward 1982). In the case of Little Owl territories, the biotope structure of pastures and meadows had this significance. Due to their relatively low vegetation height throughout the year, these areas offered a continuous food supply (e.g. voles, earthworms, carabids) to the Little Owls in all seasons. However, it must be noted that no direct correlation was found between the areal portion of such biotope structures within the territories and the absolute size of territories. Kenward (1982) had found this direct correlation in the home ranges of Goshawks. Nevertheless, the territorial borderlines of Little Owls sometimes coincided with the boundaries of pastures and meadows (i.e. fences, ditches, roads). This was especially so in summer when territories of minimum size were defended. In this season, the shape of territories in some cases seemed to be directly influenced by these external structures.

A number of authors have discussed in detail how habitat quality, particularly the availability of food, can influence territorial behaviour and territory size. Some maintain that there is an inverse relationship between the quality of habitat (e.g. food supply) and the territory size (Clark 1975; Kluyver and Tinbergen 1953; Klomp 1972; Krebs 1971; Lockie 1955; Newton 1979; Southern 1970; Stephan 1976). Lack (1968), however, disputes that the territory size is primarily controlled by the factor of availability of food. If the food supply actually influences the territory size, this influence should differ in its significance in species with short-term territories or with long-term territories, respectively. If other factors do not interfere (e.g. population density), the size of short-term territories could be newly fixed at the beginning of the territorial period and, therefore, more easily adjusted to the actual food situation. Tenants of long-term territories, however, would be confronted with the problem as to which season or year they should select for the adjustment of the size of their territories. A territory that might optimally serve the requirements of its tenant in spring of one year could be far out of dimension in other seasons or years, when the availability of, or the demands for food have changed. Patterson (1980) stipulates that the size of long-term territories, in contrast to that of short-term territories, should not exhibit any major response to short-term changes in resource abundance. He suggests that only long-term changes in the availability of food will lead to an adjustment of territory size to the altered conditions. Thus, tenants of long-term territories should generally defend even an excess of those resources they need for survival and reproduction (MacLean and Seastedt 1979; Rush and Reeder 1978; Myers et al. 1979).

With regard to the territory sizes of Little Owls during different periods of the year, this study revealed, on the other hand, that the defended area and their territorial behaviour were subject to seasonal variations. Such variations, so far, had been observed in short-term territories during the breeding season (Ickes and Ficken 1970; Knapton and Krebs 1974; Krebs 1971; Nice 1937; Moeller 1987; Stefanski 1967; Tompa 1962), but had also been postulated to exist by some authors for long-term territories (Kalela 1958; Klomp 1972; Lendrum 1979; Newton 1979). In case of the Little Owl the causes of this variation in territory size and territorial aggressiveness can be seen in relation to the breeding cycle.

Furthermore, the varying requirements of nourishment in different seasons with changes in food availability were determined to be an important factor.

In early spring, when the availability of food increases after the winter low, the courtship season of Little Owls starts and the males reach the peak of their aggressiveness. Large territories were seen to be established which would find their limits in the economy of their defendability towards competitors (Brown 1964; Davies and Houston 1984). Therefore, the intensity of competition also plays a major role (e.g. correlated to the population density, Village 1982).

With the beginning of the breeding season the condition changes in so far as a higher demand of food has to be satisfied by the territorial males. Their mates and, later on, their offspring have to be fed. Therefore, less time and energy are left for the defense of territories. Consequently, the territory size decreases.

In summer, when the fledglings are still fed within the parental territory, the conditions continue to be in disfavour of the time and energy that can be spent for territorial defense. There is a continuously high demand for food. In addition the situation may be aggravated both by unfavourable feeding conditions and by the physiological stress of the starting moult of the adult birds (Exo 1987; Exo and Hennes 1980). Consequentially, in these months the male Little Owls reach their all year minimum in body weight (Exo 1987, 1988; Finck 1989) and the smallest territories are defended. A low level of aggressiveness following the breeding season has also been observed in other bird species (e.g. Nice 1937). Kalela (1958) characterizes this period as "refractory phase". In birds with short-term territories, territorial behaviour ceases completely. They develop a gregarious behaviour (Zimmermann 1971) and do not resume their territorial behaviour before autumn (Hailmann 1960; Snow 1956; Tompa 1962) or the next courtship season. The observed low level of aggressive behaviour of Little Owls in the summer months also has the effect that the fledglings are tolerated in their parental territories for a number of weeks.

In autumn, the adult males again become more aggressive. This season is characterized by an increasing potential prey density (i.e. voles, mice and earthworms) and by an increasing accessibility of the prey due to low vegetation height (Exo 1988). The first-year birds have been expelled from the parental territory and become independent. The rate of intruders into the adults' territories increases due to the rising number of roving first-year Little Owls (Exo 1987, 1988) that try to establish a territory of their own. Exo also observed that in this period the frequencies of territorial calls uttered by Little Owls increased again after it had reached an all year minimum in summer. In autumn, adult males have to extend their territories to secure their food in winter.

During periods of warm weather in winter with no snow cover on the ground, a smaller amount of time and energy has to be expended by Little Owls for the daily nourishment. Under these conditions the territories of Little Owls were seen to be almost similar in size to the territories defended during the courtship season. Periods of coldness with a ground cover of snow caused difficult feeding conditions and a loss of body weight. Consequently, the territorial aggressiveness decreased and ceased completely when conditions deteriorated even further. This was also observed in winter territories of other bird species (Knapton and Krebs 1974 and Nice 1937 on Song Sparrows; Scott 1984 on Mute Swans; review by Kalelea 1958). In summary, the lower threshold for the occurrence of territorial behaviour (Carpenter 1987) in winter is approached or reached due to the strained energetic conditions.

Other factors, in addition to the changing behavioural time budgets, contributed to the observed seasonal variation of territory size. Thus, individual differences in territorial aggressiveness (Finck in prep.) seemed to cause some modifications in territory size. Furthermore, Little Owls with little experience in the area they occupied, defended larger territories than experienced tenants (Finck in prep.). On the other hand, in this study population density seemed to have only minor effects on the territory size of Little Owls. Although birds living in population densities ranging from 0.75 ♂♂/km^2 to 2.25 ♂♂/km^2 were studied, no consistent differences in territory sizes were detected. The observed seasonal differences in territory sizes, however, were found in all studied birds irrespective of individual differences in aggressiveness, of differing time of experience in the occupied area or of the differences in population density.

In the course of the study it became evident that Little Owls are able to quickly react to changes in the accessibility of certain allotments in their environment by quickly shifting their hunting ranges, even beyond their territories. This observation was also made by Exo (1987). The territorial boundaries, on the other hand, were by far not as promptly altered in reaction to changing accessibility of food (e.g. sudden changes in vegetation height due to mowing or harvest). This behavioural flexibility has the advantage that newly appearing food sources can be exploited. On the other hand, the more conservative retention of the territory boundaries secures the long-term nourishment in case these new food sources are only of temporary value.

Acknowledgements. My thanks go to Prof. Dr. D. Neumann for critical discussions and his support throughout the study. I am grateful to the many landowners whose farms were used during the study. U. Riedel kindly corrected the English version. This study was financially supported by the Ministry of Science and Research, NRW, and by a graduate student grant of the state of NRW to the author. This paper presents part of the author's doctoral thesis (Finck 1989) at the University of Cologne.

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