

Synurbization - adaptation of animal wildlife to urban development

Maciej Luniak

Abstract

Recent zoology/ecology coined a new term, synurbization, as an analogy to the existing term of wider meaning – “synanthropization.” Synurbization denotes adjustment of wild animal populations to specific conditions of urban environment. The new term, was introduced by theriologists and it is accepted in ornithology as well. The term “urbanization,” in turn, should be in ecology applied for changes in landscape (or environment) caused by urban development. The growing and global tendency towards synurbization, observed recently in animal world, is a response to world-wide expansion of urban development (urbanization). More and more bird and mammal populations colonize cities, and some of them are in urban conditions much more successful than in their native natural habitats. In Europe, the best known examples are black-bird *Turdus merula*, magpie *Pica pica*, Hooded crow *Corvus corone cornix*, kestrel *Falco tinnunculus*, red squirrel *Sciurus vulgaris*, Striped field mouse *Apodemus agrarius*, rabbit *Oryctolagus*, red fox *V. vulpes*. In Warsaw, during the past few decades, at least 12 new bird species and 2 mammal species have colonized areas of high degree of urbanization. Synurbic populations show several significant ecological and behavioural differences, as compared with populations of the same species living in their native non-urban habitats. Among most typical features of synurbization are: higher density of population connected with reduction of individual (pair, family) territories, reduced migratory behaviour, prolonged breeding season (even winter broods) and other changes in breeding ecology, prolonged and changed (sometimes adversed) circadian activity, increased longevity (but worse health parameters!), changes in diet and in foraging behaviour, increased intraspecific aggression, tameness toward man and various adaptations to human behaviour. All the above adjustments of synurbic populations seem to be within the range of natural plasticity of the species. The question concerning possible genetic differences between synurbic and non-urban populations has no clear answer so far.

The rapid increase of the phenomenon of synurbization, which is observed in recent decades, shows chances for coexistence between wild animals and our urban civilization. It also shows possibilities for managing of wildlife in cities. But it does not change the fact, that a world ecological crisis affects the fauna in cities just as in the animal world as a whole.

INTRODUCTION

Recent decades have seen an increasing tendency for birds and mammals to colonize cities. This phenomenon posed the need for a new term - *synurbization*, which was created by theriologists-ecologists (Andrzejewski et al. 1978; Babińska-Werka et al. 1979). It denotes an adjustment animal populations to specific conditions of the urban environment, in connection with regular existence (often breeding) there in the wild state. The term is not applied to individual animals which have come (or been brought by humans) to an urban area accidentally and which live there for a limited time. Synurbization is related to

two other terms used in this field: *synanthropization* and *urbanization*. Synanthropization refers to the adaptation of animal populations to human-created (anthropogenic) conditions in general and urbanization refers to changes in landscape (environment) caused by urban development. Therefore, synurbization is the particular case of synanthropization under the specific conditions of urbanization.

The phenomenon of synurbization has been described mainly for birds and mammals, but it is known also in other animal groups (e.g. amphibians).

Author's address: Institute of Zoology, Wilcza 64, PL 00-079, Warszawa, Poland

It is a subject of increasing interest to science, because it demonstrates ecological and behavioral plasticity and microevolutionary changes in animal populations under anthropogenic pressure. It is also a point of interest in applied ecology, because it implies the possibility of enriching and managing urban wildlife.

This paper presents characteristic features of synurbic populations. Eusynanthropic species living in cities - e.g. the house sparrow (*Passer domesticus*), house mouse (*Mus musculus*), brown rat (*Rattus norvegicus*) and feral pigeon (*Columba livia f. urbana*) - will be not considered here, as they are not comparable with rural populations. Among general reviews on the topic are those of Gliwicz et al. (1994) and Luniak (1996).

THE PHENOMENON

More and more bird and mammal species, represented by growing numbers of local populations, are settling and increasing their abundance in cities. In Warsaw (Poland), at least a dozen bird species (Table 1), and 2 mammal species (the rabbit - *Oryctolagus oryctolagus* and the striped field mouse - *Apodemus agrarius*), have colonized highly urbanized areas since the middle of the century. Examples of synurbization of mammals in European cities are provided by the squirrel (*Sciurus vulgaris*, *S. carolinensis*), the rabbit, the striped field mouse, the red fox (*Vulpes vulpes*), the stone marten (*Martes foina*), and the badger (*Meles meles*). Processes of synurbization also concern wild populations of birds introduced (or reintroduced) to cities by man. The best known example is the peregrine falcon (*Falco peregrinus*), which has been successfully introduced, in the last two decades, to cities in North America and in Germany, as well as Prague, Warsaw and Moscow. Introduction of the peregrine into cities has supported the natural recovery of the overall population of this species. Urban populations of peregrines on both continents have increased rapidly and are now much bigger than ever. New York and Berlin have the highest concentration of peregrine falcons in the world.

The phenomenon discussed also concerns feralized populations originating from escaped or released cage birds. Among the birds which have the most stable wild populations in several European cities are the Mandarin duck (*Aix galericulata*), Canada goose (*Branta canadensis*), ring-necked parakeet (*Psittacula crameri*) and common myna (*Acridotheres tristis*). The possible scale of this phenomenon is shown by data from Tokyo and its vicinity, where 71 feral bird species were reported in the period 1961-1981, 20 of them breeding in the wild (Narasue and Obara 1982). It is expected that the significance of this factor to urban avifauna will increase in the future.

TAKING UP A FREE ECOLOGICAL NICHE

Synurbization is a wildlife response to global expansion of urbanization. The majority of contemporary fauna species shaped their ecological and behavioral status during the last 1 to 500 million years, while urbanization, in the scale of landscapes, has occurred only during the last 100-200 years. In terms of nature, cities are "explosion" of new and "strange" type of environments (complex of habitats, landscape) characterized by the highest anthropogenic pressure. Urban development destroys natural habitats, but also creates new, free ecological niches covering areas which grow rapidly. This expanding "ecological vacuum" attracts more and more animal populations. Some of them overcome the ecological barriers posed by urbanization and adapt successfully to specific conditions offered by the new niche.

Among the main pre-requisites for synurbization are general ecological, demographic and behavioral plasticity, particularly a wide spectrum of habitat and diet requirements.

In European fauna, the best-known example of the expansion of synurbic populations to cities is the European blackbird (*Turdus merula*) (Luniak et al., 1990). This species used to be entirely a forest bird, but it began to colonize urban parks in western regions of Germany in the first decades of 19th century (in Bromberg - 1820, Augsburg - 1830, Frankfurt/M. and Stuttgart - about 1850). The expansion continued, and at the beginning of 20th century, it reached western territories of present Poland (Gdańsk, Poznań, Silesia). By the middle of the century it reached the line Kaliningrad - Warsaw - Brno - Sofia. Recently the northeastern range of the urban blackbird population includes Oslo, Helsinki, St. Petersburg (Russia), Kiev and Poltava (Ukraine). At the same time, the synurbization of Asiatic subspecies of the blackbird is being observed. *Turdus merula aterrimus* has begun to settle in towns in Turkey (Istanbul, Ankara) and in the Caucasus (Yerevan, Tbilisi, Cherkesk), while *T.m.intermedius* is colonizing cities in Kazakhstan (Alma-Ata, Samarkand, Tashkent). The synurbic population of the blackbird has not yet occupied areas of the northeastern range of the species being as yet absent in Moscow. Blackbirds are common in the region. Nevertheless the speed and spatial range of the expansion of synurbic blackbirds are comparable with the most intensive zoogeographic expansions noted in vertebrates - like the collared dove (*Streptopelia decaocto*) and muskrat (*Ondatra zibethica*) in Europe, or the house sparrow (*Passer domesticus*) and starling (*Sturnus vulgaris*) in North America. In all cases known, the natural colonization of new towns by the blackbird was firstly by wintering birds, which then stayed for breeding. Big cities were usually inhabited

by the blackbird earlier than small towns in the region.

Examples of the rate of growth of synurbic populations are magpie (*Pica pica*) and fieldfare (*Turdus pilaris*) in Warsaw. The magpie (Luniak et al. 1997) was practically absent from the inner city until the 1950s, and only a few pairs bred there at the beginning of 1960s. In the 1970s, the estimation was 50-200 breeding pairs, and in the 1980s, an increase to 800-1200 pairs breeding was recorded in a 52 sq. km plot in the inner city. In 1990s, the growth of population continued. In three decades the magpie achieved the sub-dominant position (2%) in the overall bird community in the highly urbanized areas of Warsaw. Fieldfares began to breed in urban parks of inner Warsaw in 1975 (<10 pairs), and within ten years (1985) had reached 80-100 pairs (52 sq.km plot). During the next 5 years (to 1990) the rate of growth was three-fold, to 250-350 pairs.

URBAN VERSUS RURAL POPULATIONS

Adaptation to urban ecological niches requires changes in the behavior and ecology of synurbic populations, in comparison with non-urban (rural) ones. In the European fauna, the best-studied species in this respect are the blackbird, wood pigeon (*Columba palumbus*), mallard (*Anas platyrhynchos*), striped field mouse and red fox. Several studies (Andrzejewski et al. 1978, Avilova et al. 1994, Babińska-Werka et al. 1979, Engel et al. 1988, Gliwicz 1980, Gliwicz et al. 1994, Luniak et al. 1990, Macdonald and Newdick 1982, Tomialojc 1976, 1978) indicate that the most characteristic adjustments of synurbic populations are the following, as listed by Luniak (1996):

- Living at much higher population density (Table 2), connected with a reduction in the size of individual (pair, family) territories. Among reasons for this are, less pressure from raptors in the city and the spatial limitations of suitable sites (green islands) surrounded by built up areas.

- Reduced migratory behavior connected with better possibilities for wintering in the city. This takes advantage of the milder urban microclimate, snow-free spaces and ice-free waters, and the rich resources of anthropogenic food, which is found as refuse or offered by the feeding public. In Central Europe, synurbic populations of the blackbird, mallard, Coot (*Fulica atra*), mute swan (*Cygnus olor*), and rook (*Corvus frugilegus*), spend winter mostly in breeding areas. Rural populations of these species, however, migrate long-distances to winter quarters. The urban striped field mouse (in Warsaw) and red fox (in England) have also demonstrated a strong tendency towards a sedentary life.

- Prolonged breeding season, mainly allowed by a

sedentary life and favorable microclimatic conditions. More time in the phenological cycle is left for breeding, the physical condition of individuals after wintering is better and some breeding sites (e.g. in buildings and other technical objects) are warmed or well sheltered against the cold. Synurbic blackbirds begin breeding 1-4 weeks earlier than rural ones, and their last fledglings leave the nest about one month later in the summer. Blackbirds in cities usually have 2-3 broods, while those in forests have 1-2. Cases of winter broods among several bird species (e.g. blackbird, collared dove, coot) have been observed in cities. Urban magpies in Western Poland build their nests 3-4 weeks earlier than rural ones, occasionally in winter (Jerzak 1995). In Warsaw, the striped field mouse shows sexual behavior in October, and even into winter, a phenomenon observed rarely in rural population of the species.

- Greater longevity connected with better winter survival due to favorable food and climatic conditions, and a reduction of migrations, which are more dangerous and more exhausting than sedentary life. Another important factor is lower predator pressure, as most raptor species are poorly pre-adapted to synurbization and avoid cities. The result is weaker individual selection in urban populations. Thus, albinotic, crippled and degenerate individuals are commonly observed in urban populations, whereas from natural habitats they are largely absent. Investigation on striped field mouse in Warsaw revealed considerably worse blood parameters (Rewkiewicz-Dziarska et al. 1977) and higher infestation by parasites (Gliwicz et al. 1990) in urban populations compared to rural ones. Urban blackbirds live 1 - 1.8 years longer than rural ones. On the other hand, birds and mammals in the urban landscape are more often victims of collisions with technical objects (traffic, glass panes, wires). But, studies on blackbirds in Vienna (Lidauer 1983) indicate a substantial percentage of individuals with healed wounds, while in natural conditions these birds would be eliminated.

- Prolonged circadian activity. This may be connected with artificial lighting or the tendency to spend the hours of most intense human activity in shelters. Urban birds begin singing earlier in the morning and finish later in the evening. In urban blackbirds, cases of nocturnal activity (singing, feeding) are known, never observed in the forest population. Feral pigeons active at night are commonly observed in cities. Conversely, the striped field mouse, which exhibits nocturnal activity in natural habitats, is active in open spaces in urban parks during the day.

- Changes in nesting habits, including the use of a variety of anthropogenic objects as shelters, nesting places and material for nests. In inner Warsaw, 81% of the overall bird population nests in technical objects, mainly in buildings. Synurbic populations of birds

tend to locate their nests higher up than rural ones. In blackbirds the mean difference is about 1 m. Mallards of inner Warsaw nest only in tree cavities and in other elevated sites (e.g. baskets on trees), never on the ground, as rural Mallards commonly do.

- Changes in feeding behavior. A city offers rich resources of anthropogenic food (refuse, feeding by people), which are attractive to many bird and mammal species. For some, (e.g., feral pigeon, house sparrow, collared dove, mallard, corvids, gulls) this kind of food is a substantial (sometimes the main) component of the diet, particularly in the winter. The feeding behavior of these birds, as well as of some mammals (e.g. park squirrels and mice, urban red foxes) is adjusted to human customs and is aimed at finding or receiving human food.

- Tameness toward people. This is the basic barrier to be crossed by vertebrates under synurbization, because coexistence with man is the condition for successful inhabiting of the city. Almost all bird and mammal species living there reduce their escape distance in comparison to that maintained in rural areas. They often follow people begging for food, or even sit on people. Many examples show that species which in natural circumstances are particularly shy towards man (e.g., raptors, waterfowl hunted by man) become tame in cities. Jedraszko-Dabrowska (1990) described aggressive reactions to man in urban coots. Such behavior is never observed in rural populations of this species.

- Increased intra-specific aggression is observed in synurban populations, a tendency connected with the high density of individual territories and spatial limitations. Such behavior is commonly observed in urban blackbirds, and it was also described by Jedraszko-Dabrowska (1990) in the coot. Laboratory tests have also revealed that urban blackbirds have better learning capability than forest ones (Walasz 1990).

The question regarding the extent to which synurban populations have their own genetic identity is still not clearly solved. Changes in ecological parameters and behavior can be explained by the direct effect of urban conditions and seem to be within the range of the species' natural plasticity. Nevertheless, morphological, anatomical and physiological differences between urban and rural populations of the striped field mouse have been found and interpreted as genetic (Gliwicz 1980, Gliwicz et al. 1990). Such differentiation was also found in the behavior of blackbirds of urban and forest origin reared in the laboratory (Walasz 1990), and also in studies by Schwabl et al. (1985) and Berthold (1984) on conditioning of migratory behavior in birds. Septon et al. (1995) found that in Midwestern North America, 90% of peregrine falcons of identified urban origin nest in cities, while 83% of peregrines reared in natural habitats on cliffs nest in such sites. It seems that

imprinting plays an important role in adjustments, which make synurban populations different from rural ones.

CHANCE FOR URBAN WILDLIFE

The main consequence of urban development for wildlife is a decrease in its species and ecological diversity. The growing tendency towards synurbization observed recently in birds and mammals is an optimistic chance for enriching diversity of urban wildlife. But, increasing synurbization processes do not change the fact that a global ecological crisis is affecting urban fauna, particularly its diversity, as well as the whole animal world. Two examples:

1) In the inner area of Warsaw, 47 bird species have decreased populations or vanished since the middle of century. In the same period, 34 species (Table 1) have increased their populations in this area, as a result of synurbization and often in connection with expansion of the geographic range of the species (data of W. Nowicki). The overall avifaunal diversity of inner Warsaw decreased, despite of the intensive synurbization processes shown by several species.

2) In Berlin, among 170 breeding bird species recorded, 97 (57%) are included in the Red List, of which 29 (17%) have become extinct, and 40 (23%) are threatened by extinction or highly endangered (Witt 1991).

Synurbization of some species could cause practical problems when their populations grow to high concentrations. Such problems cause roosting of starlings (*Sturnus vulgaris*) and corvid birds (*Corvidae*) in cities. Winter roosting concentration of rooks (*Corvus frugilegus*) and other corvids in Warsaw were estimated at approximately 250 thousand of birds (Luniak 1990), and in Moscow, approximately 800,000 (Ilychev et al. 1987). An example of such problems is the Canada goose in North American cities.

Current scientific knowledge, and practical experiences, offer wide range of possibilities to stimulate, and to control synurbization processes. Cities could be refugee and conservation areas for some endangered species. A spectacular example of this is recovery of the peregrine falcon. Successful recovery in North America and Europe of this nearly extinct bird is connected with rapid growth of its urban population. In this case synurbization of peregrine was stimulated by introduction of this species in many cities and protection measures taken there.

Managing urban wildlife by stimulation and control of synurbization processes should be aimed to support natural functions and structure of the city ecosystem, with ecological and social needs of man and with the general strategy of nature conservation in mind.

CONCLUSIONS

The term "synurbization" denotes more precisely the phenomenon of the adjustment of animal populations to the urban environment than the term "urbanization," which should be applied to changes in the landscape caused by urban development.

The synurbization of bird and mammal populations is an increasing phenomenon worldwide. It is a response of wildlife to the global explosion of urbanization, which creates new ecological niches acceptable to some animal species. Synurbic populations are distinguished from rural ones in relation to several specific ecological and behavioral features. In some cases morphological, physiological and parasitological differences between urban and non-urban populations were revealed. These adaptations seem to be within the biological plasticity range of the species. Imprinting probably plays an important role in synurbic adjustments. But, evidence was also found suggesting genetic differences distinguishing urban populations.

The increasing phenomenon of synurbization shows that there are chances for some kind of coexistence between nature and expansion of urban civilization. It does not, however, change the fact that an ecological crisis is affecting the fauna in cities just as in the animal world as a whole. Present knowledge offers possibilities for enriching poor diversity of wildlife in cities, and to manage it with city dwellers' needs and general strategy of nature conservation in mind.

REFERENCES

- Andrzejewski, R., J. Babińska-Werka, J. Gliwicz and J. Goszczyński. 1978. Synurbization processes in an urban population of *Apodemus agrarius*. I. Characteristics of population in urbanization gradient. *Acta theriol.* 23: 341-358.
- Avilova, I.V., B. B. Korbut, and S. Ju. FOKIN. 1994. [Urbanized population of waterfowl (*Anas platyrhynchos*) of the Moscow city]. Izd. Mosk. Univ., Moskva.
- Babińska-Werka, J., J. Gliwicz, and J. Goszczyński. 1979. Synurbization processes in an urban population of *Apodemus agrarius*. II. Habitats of the Striped Field Mouse in town. *Acta theriol.* 26: 405-415.
- Berthold, P. 1984. The control of partial migration in birds: a review. *Ring* 10: 253-265.
- Engel, J., M. Keller, J. Leszkiewicz, and J. Zawadzki. 1988. Synurbization of the mallard *Anas platyrhynchos* in Warsaw. *Acta orn.* 24: 9-28.
- Gliwicz, J. 1980. [Ecological aspects of synurbization of Striped Field Mouse *Apodemus agrarius* (Pall.)]. *Wiadomości Ekol.* 26: 185-196.
- Gliwicz, J., J. Goszczyński, and M. Luniak 1994. Characteristic features of animal populations under synurbization - the case of the Blackbird and of the Striped Field Mouse. *Memorabilia zool.* 49: 237-244.
- Ilyichev, V. D., B. T. Butyev, and M. B. Konstantinov. 1987. Birds of Moscow and its vicinity. Izd. Nauka, Moskva.
- Jerzak, L. 1995. Breeding ecology of an urban Magpie *Pica pica* population in Zielona Góra (SW Poland). *Acta orn.* 29: 123-133.
- Jedraszko-Dabrowska, D. 1990. Specific features of an urban lake bird community (case of the Czerniakowskie Lake in Warsaw). In: Luniak, M. (ed.), Urban ecological studies in Central and Eastern Europe. Ossolineum, Wrocław, pp. 167-181.
- Lidauer, R. M. 1983. Knochenfrakturen bei Stadtamseln (*Turdus merula*). *Oekol. Voegel* 5: 111-126.
- Luniak, M. 1996. Synurbization of animals as a factor increasing diversity of urban fauna. In: di Castri, F., and T. Younes (eds.). Biodiversity, science and development: towards a new partnership. CAB International, pp. 566-575.
- Luniak, M., P. Kozłowski and W. Nowicki. 1997. Magpie *Pica pica* in Warsaw abundance, distribution and changes in its population. *Acta orn.* 32: 77-87.
- Luniak, M., R. Mulsow and K. Walasz 1990. Urbanization of the European Blackbird expansion and adaptations of urban population. In: Luniak M. (ed.), Urban ecological studies in Central and Eastern Europe. Ossolineum, Wrocław, pp. 87-199.
- Mac Donald, D. W., and M. T. Newdick 1982. The distribution and ecology of foxes, *Vulpes vulpes* (L.) in urban areas. In: Bornkamm, R., J. A. Lee, and M. R. D. Seaward (eds.). Urban ecology. Oxford Univ. Press, Oxford, pp. 123-138.
- Narasue, M., and H. Obara 1982. Feralization of cage birds, in and around Tokyo. In: Numata, M. (ed.). Chiba Bay-Coast Project, IV. Tokyo, pp. 82-86.
- Rewkiewicz-Dziarska, A., Wielopolska , A. and J. GilJ. 1977. Hematological indices of *Apodemus agrarius* (Pallas 1771) from different urban environments. *Bull. Acad. Pol. Sci.*, 25: 261-268.
- Septon, G., J. B. Marks, and T. Ellestad. 1995. A preliminary assessment of Peregrine Falcon *Falco peregrinus* recovery in Midwestern North America. *Acta orn.* 30: 65-68.
- Schwabl, H., J. C. Wingfield, and D. S. Farner 1985. Influence of winter on endocrine state and behaviour in European Blackbirds (*Turdus merula*). *Z. Tierpsychol.* 68: 244-252.
- Tomialojc, L. 1976. The urban population of the wood pigeon *Columba palumbus* Linneaus 1758 in Europe - its origin, increase and distribution. *Acta zool. cracov.* 21: 586-631.
- Tomialojc, L. 1978. The impact of predation on urban and rural wood pigeon (*Columba palumbus*) populations. *Polish ecol. Studies* 5: 141-220.
- Walasz, K. 1990. Experimental investigations on the differences between urban and forest blackbirds. *Acta zool. cracov.* 33: 235-271.
- Witt, K. 1991. Rote Liste der Brutvoegel in Berlin, 1. Fassung. *Berl. Ornithol.*

Table 1. Examples of bird species which have colonized Warsaw recently, as a result of their synurbization (not as a geographical expansion). * - non-breeding species.

Spp. advanced in synurbization	Spp. less advanced
Mallard (<i>Anas platyrhynchos</i>)	Mute Swan (<i>Cygnus olor</i>)*
Black-headed Gull (<i>Larus ridibundus</i>)	Kestrel (<i>Falco tinnunculus</i>)
Blackbird (<i>Turdus merula</i>)	Common Gull (<i>Larus canus</i>)*
Fieldfare (<i>Turdus pilaris</i>)	Wood Pigeon (<i>Columba palumbus</i>)
Hooded Crow (<i>Corvus cornix</i>)	Jay (<i>Garrulus glandarius</i>)
Magpie (<i>Pica pica</i>)	Hawfinch (<i>Coccothraustes coccothraustes</i>)

Table 2.Examples of differences in density of populations - rural versus urban ones. PL - data from Poland, x - multiplication.

Species, locality	Rural: <u>Urban</u>	Author
Blackbird (<i>Turdus merula</i>), PL	0.5-3 p./10 ha <u>x>20</u>	Luniak et al.1990
Wood Pigeon (<i>Columba palumbus</i>), SW PL	0.1-7 p./10 ha <u>x 10-30</u>	Tomia ³ ojæ 1980
Magpie (<i>Pica pica</i>), SW Poland	0.2-0.6 p./10 ha <u>x 20-50</u>	L.Jerzak, Luniak et.al.1997
Hooded Crow (<i>Corvus corone</i>), Moscow	3-10 ind./km sq. <u>x 20-60</u>	Ilyichev et al.1987
Reed Warbler (<i>Acrocephalus arundinaceus</i>), PL	2-5 p./1 ha <u>x 2-6</u>	Jêdraszko-D'browska 1990
Coot (<i>Fulica atra</i>), PL	4-5 p./1 km of shore <u>x 2</u>	Ibidem
Peregrine Falcon (<i>Falco peregrinus</i>), Berlin, N.York	<u>x>5</u>	
Striped Field Mouse (<i>Apodemus agrarius</i>), PL	4-8 ind./ha <u>x 5-10</u>	Gliwicz et al. 1994
Red Fox (<i>Vulpes vulpes</i>), England	<0.1 fam./km sq. <u>x>10</u>	MacDonald, Newdick 1982
White-tailed Deer (<i>Odocoileus virginianus</i>), USA	8-11 ind./ml sq. <u>x 7-18</u>	Adams 1996